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The Whole Fungus

Volume 1

Edited by Bryce Kendrick

1979
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The Whole Fungus

Kananaskis II

The Whole Fungus

The Sexual-Asexual Synthesis

Proceedings of the
Second International Mycological Conference
held at the Environmental Sciences Centre of the
University of Calgary
Kananaskis, Alberta, Canada

Edited by Bryce Kendrick

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For those mistakes and misinterpretations that have inevitably crept into this book, I accept sole responsibility.

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1
Introduction

Bryce Kendrick

The fungi are at last coming into their own. Their unique biochemistry and lifestyle have now been recognized by the introduction, and widespread acceptance among biologists, of a separate kingdom -- Fungi. This must have come as something of a shock to many mycologists who had become accustomed to being treated as peripheral, both to the main thrusts of biological thought and, perhaps even more important, its administrative subdivisions. Most of us who teach in Biology Departments have been thought of as appendages of the botanical fraternity. And we have usually accepted this role, probably for lack of any viable alternative. Now it is up to us to assert our new-found independence. Since we are a small minority among the biological fraternity, this assertion must be both subtle and rational. It would be neither politic nor practical to secede unilaterally. That would simply be counter-productive. But I think there may some day be Subdepartments or even Departments of Mycology just as there are Departments of Bacteriology today.

How can I base such a forecast on the simple accession of our discipline to a still largely theoretical throne? Would we not be likely to share the fate of 'The Man Who Would Be King'? Fortunately, our case is not built on theory alone. In recent years the practical importance of the fungi has become more and more obvious. We mycologists have always known of, and have doubtless spoken eloquently about, their vital role in the silent, all-pervading but largely invisible processes of biological recycling. But other biologists are becoming increasingly aware that fungi are important to their disciplines. Here are some examples.

The ecology of streams and ponds has acquired a new dimension with the discovery that the fungi are vital intermediaries in energy flow, 'conditioning' the allochthonous organic matter which is often the main energy base of these systems, and making it both palatable and nutritious to the detritivorous benthic invertebrates.

While it was once assumed that the bacteria did most of the work in sewage treatment, we now know that there is an enormous fungal biomass at work, and there is even some suggestion that this may play a dominant role in the trickling filter and activated sludge processes.

Medical mycology has undergone a resurgence in recent years because of the universal use of antibacterial antibiotics, and the consequent emergence and recognition of certain mycoses as an intractable, or at least troublesome, residuum. The advent of immunosuppressive therapy for certain serious medical problems has given some opportunistic fungal pathogens the

chance they needed to invade, and sometimes kill, the defenceless patient.

The pathogenic activities of fungi on Man's crop plants has been important since the dawn of agriculture. But with increasing mechanization, and the concomitant spread of monocultures over huge areas, the harmful potential of fungal plant diseases has automatically been augmented.

Growing concern with environmental toxicology, generated largely by the widespread use of pesticides and fungicides, has generated increased interest in biological control. The parasitic activities of many fungi on plants (weeds), arthropods (pests) and other fungi (pathogens) make them of actual or potential importance in this field.

Toxicologists have recently become aware that the growth of some common moulds on foodstuffs leads to their contamination with dangerous -- even carcinogenic -- fungal metabolites such as Aflatoxin. This has invested those fungi that attack stored food with a new and more sinister significance.

We now know that the vast majority of higher plants, with the exception of a few weedy families, are mycorrhizal, and that the fungi involved can materially assist the plant to obtain phosphorus from soils deficient in that element.

Fungi are being increasingly exploited by industry for the enzymes, organic acids, vitamins, antibiotics and other useful substances they produce.

And I cannot leave out the cultivation of agarics and yeasts for food, since these are industries of some substance.

But of course we shall know that our discipline has really arrived when the layman no longer asks 'What's mycology?', and recognizes that the fungi comprise more than the familiar 'mushrooms and toadstools'.

As the Kingdom Fungi becomes an undoubted 'eminence grise' (though not, on balance, a 'bête noire'), more and more demands are being made on systematists. Identification, of species pathogenic to plants, animals and humans, of toxin-producers, and of many other ecologically important taxa, has become increasingly important. And, because science always seeks patterns amid diversity, so has the need for an over-all, unifying, predictive scheme of classification for these organisms.

The charge is sometimes levelled that taxonomy is not science but stamp-collecting, that it is concerned mainly with the accumulation of superficial observations and their arrangement in patterns that please the arranger, and that it is largely irrelevant to the concerns of science with a capital S. Like many such outrageous statements, this one contains a grain of truth. At certain levels of the taxonomic hierarchy, the decisions of reputable individual taxonomists as to what constitutes, or delineates, taxa, can be intensely personal statements, whose nature depends on whether their author is a 'splitter' or a 'lumper' at the time (people can drift slowly between these extremes with the passage of time). But although such taxonomic decisions may be idiosyncratic, and though they may remain unchallenged for years, in the long run the self-pruning feature that so clearly differentiates science from most other human activities will come into play. Because it is my belief that biological systematics incorporates and reflects -- or must at least take into account -- the full range of biological knowledge. As the scope of this knowledge increases, so the number of possible alternative phylogenies (and thus the number of alternative phyletically based classifications)

shrinks. We are still far from agreement about the ultimate shape of our taxonomic scheme (and about the nomenclature with which to express it) -- any reader of this book will be made forcefully aware of those realities. But today when we argue, we often do it from a far more rational base than would have been possible even at the time of Kananaskis-I. And make no mistake, we are now accumulating the evidence we need at an unprecedented rate. When I began preparations for Kananaskis-II, no Coelomycetes with basidiomycetous affinities were known. Now we have three examples (not all published, as yet). New information on fungal biochemistry, genetics, physiology, ecology, and anamorph-teleomorph relationships, is appearing almost weekly. And although we have not yet reconciled our various taxonomic systems (particularly of Ascomycetes), the germs of such a reconciliation already exist. We may still have to cope with two, or a few, contending schemes, but we do not carry the burden of accumulated theories that weighs down, for example, the psychologists, who have obviously found it more difficult to test and prune their hypotheses than to generate them. This advantage should not make us smug -- merely thankful that the data we need are apparently more accessible.

But the facts still do not of themselves or by themselves create a system for us. That is one of Man's conceits (as they used to be called, with uncomfortable accuracy). We now prefer to call such things concepts -- a word with a more objective ring to it. There must still, however, be room for the intuition born of experience, and the often rather divergent ideas expressed in this book show that the boredom born of unanimity and uniformity has not yet set in among mycologists.

Nonetheless, the message is that fungal taxonomy is becoming more scientific and, because science aims for predictive generalizations, more satisfying to its practitioners as well as more useful to its potential customers. But we have some unique problems.

The idea of a single genotype with two or even more very different phenotypes is certainly wonderful, but it is hardly strange. Every child over the age of five is familiar with the caterpillar which will change into a butterfly, the tadpole which will become a frog. But those changes, and thousands like them, have the feeling of inevitability about them. We know that caterpillars can't choose to remain caterpillars just because they like eating and wish to continue this delightful activity. We know that there is an internal clock which determines when the metamorphosis will take place. And our children can await its onset with a pleasurable thrill of anticipation. But what of an organism that may metamorphose *or may not?* What of an organism that may stubbornly maintain two (and sometimes more) different, separate but absolutely contemporary phenotypes? The fungi are such creatures, and Kananaskis-II concerned itself with the problems raised by such intransigence and individuality. The title of this book says, in a nutshell, what our aim was and is -- to reunite the different phenotypes, at least conceptually, and to use all of the data thus made available in the elaboration and refinement of our classificatory schemes. What the title does not say is that we have only begun, and that our first attempts, as documented in this book, are still the uncertain and poorly directed steps of a child learning to walk. But just as the child persists, so shall we. Our feet are now resolutely set on the path to a unified scheme, and I hope mycologists at large will join us on our pilgrimage. The lists of sexual-asexual connections (Chapters 17 and 20) are the most comprehensive yet published, incomplete and

inaccurate as they may be. Here is a start, here are some ideas, some analyses, some syntheses. I dedicate them to the next generation -- the holomycologists -- who will be trained to look at things from both sides.

As the progenitor of the first Kananaskis Conference in 1969, I found the meeting an authentic high -- almost a transcendental experience. I remember an ambience of excitement, a feeling of camaraderie, and a sustained intellectual intensity. I can only hope that some traces of that spirited interplay can be detected in the book 'Taxonomy of Fungi Imperfecti' that eventually arose from the Conference. Because once the curtain came down on those halcyon days and we exchanged that clear, rarefied atmosphere for the (relative) smog of our normal daily round, it grew increasingly difficult to recapture the authentic Kananaskis feeling. Tape transcription dragged on over weeks and then months. Authors wanted more time to re-cast their chapters. Editorial conferences proliferated. And when the book finally appeared (an event satisfying in itself) the Editor could have been forgiven for swearing off such activities for life.

As I now look back on Kananaskis-II, and as its book slowly grinds toward publication, I find myself wondering why I had 'let myself in for it' again. Why, after the drudgery of editing and proofreading a 300-page book am I now engaged in a lineal descendant ('Son of Kananaskis') that looks as if it will be about twice as long? Perhaps authors and editors should admit to some masochistic tendencies. Perhaps there is a need to expiate some nameless sin; perhaps there is an eremitic undercurrent in us. Certainly work on this book has cut me off at times from the several spheres of research being pursued by my students and colleagues in my laboratory. It has caused other worthy projects to be delayed or shelved for the duration. And yet I probably would not have had it otherwise. I believe that the efforts, of authors and editor, that went into the first book were not wasted. Despite an outrageously high price, that title is now almost out of print. And Kananaskis-II was just as exciting as I thought it would be. I am delighted to be able to bring you the thoughts of my colleagues at the Conference, and of those who have subsequently provided supplementary chapters.

There seems to have been a certain inevitability about the whole thing. Almost before the ink was dry on the Kananaskis-I book, people began to ask me 'When is Kananaskis-II going to be?' and 'What will it be about?' Such questions, if repeated often enough, have a tendency to generate answers. Kananaskis-I had followed the Seattle Botanical Congress. Eight years later, Kananaskis-II convened after the Tampa Mycological Congress (IMC2), and ran from September 8th - 13th, 1977, at the Kananaskis Environmental Sciences Centre of the University of Calgary. Once again Dr. Dennis Parkinson was instrumental, not merely in making local arrangements, but in supplying logistical support without which the Conference would have been much less enjoyable, and might not, in fact, have taken place at all.

The venue was as breathtakingly beautiful as we remembered it; the weather was of truly 'Indian Summer' opulence, an ideal combination of crisp, frosty nights and warm, expansive, sunny days; those gathered together were among the cream of systematic mycologists. Even the fungi collaborated, fruiting prodigally in the local forests after an unusually wet summer: before and during the Conference we ran many short but extremely productive impromptu forays. In short, all environmental factors combined to set the scene for a

fruitful meeting.

Perhaps by posing a few questions I can give you some idea of what you may expect to find as you browse through the twenty-seven chapters that follow.

Do you know what anamorphs, teleomorphs and holomorphs are? These terms are central to the theme of the book, and are defined in Chapter 3.

Do you know for how long the phenomenon of pleomorphism has exercised the minds of mycologists; and how ancient it is? These questions are answered in Chapters 2 and 26, respectively.

Do you know how to differentiate scolecospores and helicospores from other Saccardoan spore types? You'll find what we hope are unequivocal delineations in Chapter 5.

Do you know that one method of conidium development can be transmuted into another; and that the same fungus can use two techniques concurrently? These important 'aberrations' are discussed in Chapters 6 and 7, respectively. Incidentally, these chapters firmly establish that conidium ontogeny cannot, after all, form the base on which a stable classification of Fungi Imperfecti might be erected.

Do you know how present-day distributions of fungi can be interpreted in terms of plate tectonics ('continental drift')? This is attempted in Chapter 8.

Do you know how classifications of ascomycetous anamorphs and teleomorphs affect one another? Chapters 9 - 12, 15 and 17 address this question.

Do you know that the basic Ascomycotan dichotomy between unitunicates and bitunicates can be challenged? Chapter 13 shows where.

Do you know that certain physiological factors stimulate sporulation in some fungi, but suppress it in others? Chapter 16 presents incontrovertible evidence.

Do you know that the 'aquatic' (or, preferably, 'amphibious') Hyphomycetes include some of the best examples of convergent evolution in the whole of the fungi? The evidence is given in Chapter 18.

Do you know that Agarics (and many other Basidiomycetes) also possess anamorphs? Chapters 19, 20 and 21 are concerned with these unjustifiably neglected life-forms.

Do you know that some 'yeasts' are entirely mycelial? Chapter 22 should convince you.

Do you know that a kind of 'dolipore' septum is found among the Zygomycetes? Chapter 23 discusses this phenomenon.

Do you know why we should stop calling the 'pseudo-taxa' of Fungi Imperfecti, 'form-species' and 'form genera'? Chapters 26 and 27 will tell you.

Has that string of questions whetted your appetite? I hope so.

It has been with a sense of excitement that I have seen this book through its period of gestation, because I now believe that the future of taxonomy in the 'higher fungi' lies in the integration of data streams which have long flowed parallel, widening and deepening with the years, but never really meeting. I think I see the first signs of a confluence.

2
Pleomorphism of Fungi as Treated in the History of Mycology and Nomenclature

L.K. Weresub & K.A. Pirozynski

> "A single well known and well developed species, correctly observed through all the stages of its growth, is of greater value than a new genus"
>
> Fries, Summa Veg. Scand. 1849, p. 427

The appropriate introduction to this meeting is the Tulasne brothers' (Tulasne & Tulasne 1861) *Selecta Fungorum Carpologia*, the theme of which, you will remember, was the presentation of "those facts and illustrations which go to prove that various kinds of fruits and seeds are produced, either simultaneously or in succession, by the same fungus". Regrettably, our age is such that few of us are familiar with this supreme classical work. Therefore, we will borrow liberally from it in this brief review, first, of the history of mycologists' awareness of the phenomenon of pleomorphism, and then, of the problems created by it in communication, in classification and nomenclature.

ITS MYCOLOGICAL HISTORY

The early mycologist could not fail to observe the diversity of propagules borne by the fungi he came to know. But his interpretation of this diversity was moulded by the Linnaean precept (Tulasne & Tulasne 1861:48) denying "that one and the same race could have different fructifications," and asserting that "the basis of fructification ... is also the basis of ... the natural classes of plants". In order to conform to this doctrine of "one (kind of) fructification/one (kind of) plant", and to preserve the hegemony of the "seed" as the product of that fructification, early mycologists had to resort to everything from a dishonest disregard of facts to ingenious intellectual acrobatics.

The foundation for establishing the precedence of one form as the significant propagule was laid in the first decade of the 19th century by Link and Willdenow, who were willing to equate "fungus spore" with "seed", provided that the spore, like the seed, was the result of fertilization. Thus arose the question of which of the fungus propagules was worthy of the rank of seed. This issue remained open for more than half-a-century; as late as 1858, Bail contended that the problem would be solved only when the answer was found to the question of whether fungi had sex. Long before that answer came, mycologists had decided what kind of propagule should rightfully represent the species. And by divine intervention or common fluke, they chose what turned out to be the sexually generated spore.

Fries's concept of pleomorphism was fuzzy and fluid, for he could not bring himself to commit the heresy of admitting that more than one kind of "seed" could occur in a single species. He advocated the concept of a gradual metamorphosis of propagules, culminating in true spores, and -- until 1849 -- maintained that fungi retaining "incompletely metamorphosed" propagules were merely "degenerate states" of the "more perfect fungi". Yet, he would not go so far as to unite these imperfectly developed forms with their completed counterparts: he named the former separately, though he classified them together.

Corda (1842:35) found, among the approximately 3000 fungi that he studied, only two that -- as the Tulasnes (1861:46) put it -- "besides true seeds had also seeds of inferior rank, i.e. conidia". In announcing the discovery of pleomorphism, Tulasne (1851) reserved the term "spores" for ascus-borne propagules, and adopted several other terms (used by Fries and others) to describe "less noble" propagules, conidia or, as he called them later, "buds resembling spores". Berkeley (1857:235, 268-269), on the other hand, to whom Ascomycetes were also the "more perfect fungi", labelled their ascospores "sporidia" in order to distinguish them from ordinary "spores".

The Tulasnes (1861) concurred that the production of free ascospores inside asci constituted a "more perfect" method of propagation and one characteristic of "the noblest Fungi". These they compared with other "finished" or "perfect plants" such as trees, etc. And, on at least one occasion, they had no doubt about the identity of another kind of propagule: on discovering conidia of *Cordyceps militaris*, they did not hesitate to describe the *Isaria* as "merely conidiiferous and imperfect".

However, neither Fries nor the Tulasnes advocated taxonomic dismemberment of species according to different phases in their life cycle. Fries, it will be remembered, "never distinguished genera, and scarcely ever species by the presence or absence of asci, when the latter [i.e., absence of asci] indicates an abnormal state" (Tulasnes 1861:55), and thought it superfluous to cite "innumerable Sphaeropsidei" that "outwardly mimic exactly the true Sphaeriae" (Tulasnes 1861:59). The Tulasnes were even more emphatic about the need to keep together all phases of the same fungus, although -- unlike Fries -- they did not consider conidial states abnormal, but thought the fungus merely "not fully developed and not bearing [the] proper fruit" of "autonomous, complete or perfect fungi". They, therefore, strongly condemned the actions of Corda (1842), Léveillé (1846), Duby (1851) and Bonorden (1851), who separated conidial and ascophorous forms according to what the Tulasnes called "a misconceived criterion". Thus, to the Tulasnes, this separate classification occurring at the same time that pleomorphism was demonstrated, constituted a denial that the "naked-spored types have each at the proper time its own ascophorous associate".

The taxonomic and nomeclatural separation ("against the laws of nature", said the Tulasnes) of sexual and asexual expressions -- a separation initiated by Corda -- is not without justification. It was Berkeley (1857:247, 282, 330-331) who noted that some "Sphaerias" existed in either ascigerous or conidial states, and he expressed doubt that all pycnidial forms could be linked with their respective ascophorous states. He would, therefore, consider such pycnidial fungi as "autonomous and perfect species", but others, correlated, simply as imperfect forms of their "Sphaeriae". The Tulasnes (1861:77) apparently agreed: "Let us grant that there are true Verticillia which never become changed into Hypomycetes or Hypocreae, may we then hold

that they are nothing else than imperfect Hypomycetes or Hypocreae? By no means, unless you speak from analogy; for every species, however lowly, was created perfect in itself ... and does not seem to us imperfect except in comparison with a nobler species". Commenting on a statement of Klotzsch about *Sclerotium durum* as "unworthy of the name of fungus", the Tulasnes (1861:105) disagreed, "unless what he means is a perfect fungus". Thus, with a general recognition and acceptance of the phenomenon of pleomorphism, separate names for asexual forms were retained, but primary importance was accorded the name given to the ascophorous form, whose characteristics were the taxonomic basis for classification of pleomorphic fungi.

The acceptance of Tulasne's doctrine "of the multiple nature of the seeds of Fungi" required "not only the strongest lenses and the acutest eyes, but also a patient, acute, and skilful mind, long continued observations, and repeated experiments" (Tulasnes, 1861:188). It therefore worried them that some mycologists accepting the doctrine of pleomorphy might be tempted to postulate affiliation without adequate evidence, so that "the pleasant edifice" of the doctrine might "be added to day by day and weighted with absurd increments, so as at length to collapse under its own weight". But in addition, they, like Fries, also feared that some mycologists might choose to disregard the doctrine and be satisfied to trust "a safe criterion" for prematurely judging imperfect states to be autonomous.

What the Tulasnes anticipated and dreaded came to pass. The fate of asexual elements as a separate group of fungi was sealed with Fuckel's (1870) recognition of "Fungi Imperfecti" and "Fungi Perfecti", and the adoption for the former of a separate class, Deuteromycetes, by Saccardo. Although the fungi classified as Fungi Imperfecti came to be considered parts, stages, states, phases or forms of sexual fungi, Saccardo classified them according to a system that replicated the one adopted for sexually reproducing species. It was a system that was intended by Saccardo to be no more than an artificial key. Nevertheless, those of his contemporaries who favoured a more natural arrangement must have been dissatisfied with such equality. This unease may have been the reason behind Schroeter's (1897:481) use of "Formgattung" (apparently from earlier use of Formgenus in palaeontology) prefixed as "FG" to the name of every genus of Fungi Imperfecti.

When International Rules were enunciated for the nomenclature of fungi (Brussels Code 1912), they dealt with the problem of naming pleomorphic fungi by proclaiming "special arrangements" in accordance with the dominating philosophy of the time. The examples that followed Art. 49 *bis* revealed this philosophy most clearly, for *Melampsora*, *Phyllachora* and *Diaporthe* were referred to as generic names for genera, whereas *Aecidium*, *Caeoma*, *Uredo*, *Polythrincium* and *Phoma* were merely names for [imperfect] states (see Rogers 1948:241, footnote). And the word "genus" is used only once with reference to these form-genera, and then in quotation marks. The distinction made is striking, almost as clear as if Schroeter's use of the prefix "FG" had been adopted. The prevailing taxonomic philosophy was entrenched in this Article. Fungi Imperfecti could be given names, but these were to be taken as only "pseudo-specific" and "pseudo-generic" names (Donk 1960a). It was the legalization of an "anatomical system" for Fungi Imperfecti, paralleling the "botanical system" of nomenclature (Hennebert 1971) for Fungi Perfecti.

Nevertheless, this legalization did mean that -- just at a time when facilities for study were expanding throughout the world -- the dispensation of international permission, if not recommendation, had been granted to mycologists to name imperfect states of fungi (in "species"

and "genera") separately from species and genera of sexually reproducing fungi. As mycology and plant pathology boomed, vast numbers of imperfect forms were discovered and named separately. Although Uredinales received names of both kinds, it was primarily Ascomycetes that were involved in the drastic segregation of forms, and ever-widening gaps divided not only these fungi but also those who studied them, splitting specialists in Fungi Imperfecti from ascomycetologists. There was a growing tendency to ignore the original emphasis on the distinction between the pseudo-taxa of Fungi Imperfecti and the taxa of Fungi Perfecti. Eventually, as consideration of phyletic relationships regained popularity, many form-taxa become liberated from the admitted artificiality that had been their base, and they began to compete for a place in a more natural classification as if they were themselves botanical taxa. Only now are we slowly returning to Tulasne's aim of grouping together, under one name, the disjunct phases of pleomorphic fungi.

Indeed, it is not the special arrangements in the Brussels Code that should be blamed for the two nomenclatural series for pleomorphic fungi. The problem of dual nomenclature (and taxonomy) surfaced with Tulasne's demonstration of pleomorphism in 1851, and even then prevented mycologists from introducing change that would disrupt the existing nomenclatural stability. The paradox of the status quo was expressed by the Tulasnes in 1861: while maintaining that it was an error when "stages of the same fungus have often been indiscreetly placed apart in different classes under different names", they admitted that "we have not yet found out what is the best view to take about the numerous fungi which so far appear to be merely conidiophorous, and what criterion is to be trusted, so that we may safely arrange them in the most suitable place in the system". Lind (1913:44) wrote of the attempts to resolve the problem: "Rostrup often occupied himself in searching for the proper relation of the higher form of fructification and the fungi imperfecti; and several mycologists are still engaged in finding the hitherto unknown relations. I have made great effort to find as many reliable statements as possible concerning this matter, thinking that, through analogical forms, it might be easy to state to a certain probability whether other connected forms belong to each other or not, when, for instance, a whole series of 'species' of *Fusicladium* have been proved to be conidial forms of species of *Venturia* it might be rather probable that all 'species' of *Fusicladium* would belong to *Venturia*". Perhaps the crux of our modern problem is that, unlike Lind, we now omit the quotation marks around "taxa" of Fungi Imperfecti, and have ceased to refer to them as "forms".

But in any case, the Brussels Code simply gave formal recognition to the customary way of handling the problem of naming pleomorphic fungi, and the adoption of the type method (in the Cambridge Rules, 1935, and on) reinforced the dichotomy of the separate nomenclatural systems, anatomical for Fungi Imperfecti and botanical for Fungi Perfecti. The dual system, or some form of it, will probably always be with us. But having reached a point where we have somewhat more data about pleomorphism than was available to Tulasne, a reassessment of our terminology and nomenclature as a reflection of our taxonomic approach may be fruitful.

ITS TERMINOLOGY AND NOMENCLATURE

In mycological terminology, "perfect" originated at the time when only one kind of propagule could be accepted as a proper "seed", and the metamorphosis of one form into the final "noble"

form was a necessary doctrine. The mature sexual product was therefore "perfect", complete by virtue of having reached its highest form -- "arrivées à leur état parfait", wrote Léveillé (1846).

However, increasing familiarity with the interrupted phenetic expressions of a single fungus led to an appreciation of the uniqueness of a phenomenon in which morphological phases are individually self-replicating and independently widespread. It became clear that this phenomenon, which we now call pleomorphism (Hennebert 1971, Savile 1969), does not involve the metamorphosis of one form into another in the life cycle of an individual, as in holometabolan insects, culminating in an adult form in which reproductive potential is achieved. Nor can the pleomorphism of fungi be equated with various other kinds of morphological discontinuity unaccompanied by reproductive capability, such as the caste system of certain social insects, defined seasonal forms, and larva vs. adult, or even with the differences in sexual vs. parthenogenetic expressions in animals, for all of which "non-genetic discontinuities" Mayr (1963) coined the term "polyphenism".

The discovery that, in fungi, self-replicating asexual phases can exist independently, separated in space and time from the sexual phase, called for prolonged observation and repeated experiments designed to disclose the full complement of a complete organism. Only when the two expressions were correlated, the asexual and the perfecting sexual phases brought together, could the fungus be considered "perfect", "a finished or perfect plant".

Therein lies the problem with the term "perfect". It bears a manifold connotation of wholeness, highest possible achievement, and flawlessness. Perfection is not only maturation and consummation but also a completeness comprising all parts; and perfecting is the process itself of arriving at this condition. Thus, it was a term adaptable to the range of ideas about pleomorphism; but having started in use to define one concept, it became ambiguous when the concept changed. At first, "perfect" referred to the point of completion of a life cycle through achievement of a sexual form of reproduction. Then it came to signify the complete life cycle: the whole fungus, passing through all forms of expression and reproduction, culminating in the sexual form. Almost certainly, when Fuckel (1870) wrote of Fungi Perfecti as "volkommen", he meant both complete in life cycle and perfected in development (ennobled?) through production of a sexual fruitbody. Those lacking this "perfect" form were incomplete, imperfect.

But there remained the problem of autonomous conidial fungi. Berkeley (1857) preferred to accept such fungi as "autonomous and perfect species" since, being autonomous, they were complete and therefore "perfect". The Tulasnes reluctantly concurred, but only because they could not admit that any of the "works of God" could be anything but flawless and thereby "perfect". Yet they could not bring themselves to acknowledging asexually propagating fungi as the equals of sexual species. To them, sexual reproduction was the "more perfect" (higher?) method of reproduction, and the fungi possessing it were automatically "more perfect" or "nobler" than their autonomous asexual counterparts. The Tulasnes expressed this conviction as strongly as they dared. And considering their upbringing and the age in which they lived, when challenging the dogma of special creation constituted major heresy, they were very forthright. Not long after, with the rise and wide acceptance of the Darwinian theory of organic evolution, those who followed the Tulasnes could accept and express the possibility of flaws

in nature.

In the first formulation of the rule governing the naming of pleomorphic fungi (Brussels Code, 1912, Art. 49 *bis*), these were described as having a "pleomorphic life-cycle" with "different successive states ... (anamorphoses, status)" which -- when they were "states of the same species" -- could "bear only one generic and specific name (binomial) that is the earliest which has been given ... to the state containing the form which it has been agreed to call the perfect form". This was followed by the explanation that "the perfect state is that which ends in the ascus stage .. in the basidium .. etc.". The care with which this Article was phrased is notable: the formulators were obviously aware of the problem with the word "perfect", and used it judiciously, stating (in effect) that, however the term might otherwise be defined, they had agreed to apply it to the form which appears in the final stage of what (by transference) would be called "the perfect state". Then came the following statement: "Generic and specific names given to other states have only a temporary value. They cannot replace a generic name already existing and applying to one or more species, any one of which contains the 'perfect' form". The emphasis is added here, but the quotation marks around the word "perfect" are in the printed version of the Article, signifying that the term was being used in a specially qualified way, presumably as "sexual".

However, no matter how the Rules used the term "perfect", it still held various meanings for scientist as well as layman. Most authors adopted the Rules' restricted meaning for "perfect", but without using the signal provided by the quotation marks; e.g., Melin & Nannfeldt (1934:403) wrote: *"Ceratostomella penicillata* Grosm. ... found to be the perfect stage of *Leptographium penicillatum* Grosm.", Bailey (1950:557): "No perfect stage of *Cladosporium fulvum* has been found", Martin (1961:153): "If a perfect stage exists ...", and Ainsworth (1973: 61): "Fungi frequently have two sporulating states, the imperfect ... and the perfect state ...". On the other hand, Bennett (1937:254-5) described an "ascigerous strain" and a "perfect strain", the latter producing conidia and sclerotia as well as ascomata. Authors such as Bennett obviously continued to use "perfect" as meaning "complete", "whole", "entire".

Arthur's (1934) discourse revealed another problem -- the interpretation of the term "state".* It was his contention that, at least as far as the Uredinales and Ascomycetes were concerned, "state" referred to cytological phase; "perfect state" to the sporophyte (diplo- or dikaryophase), "imperfect state" to the gametophyte (haplophase). Rogers (1948) took issue with this interpretation and clearly demonstrated its unfeasibility, even in the Uredinales. He then went on to argue persuasively that a reading of the Article and the examples that followed it could lead to only one conclusion, viz. that "the 'states' referred to by the Rules are ... organs of fructification (or assimilation)".

In the next substantial rephrasing of the Article (Stockholm Code, 1952, Art. 69),

(i) all reference to "stage" had been eliminated, along with the word "successive", because it was obviously false to imply that there was a necessary succession of these sporulating forms in the life cycle of a pleomorphic fungus;

(ii) the quotation marks around the word "perfect" were removed, the formulators apparently under the impression that all mycologists were satisfied to adopt the restricted meaning

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* Altogether unfortunate in this context since the Code uses *status* for level or position in the taxonomic hierarchy, as in *stat. nov.*

implied by the use of the quotation marks, which were therefore no longer necessary;

(iii) the term "form" disappeared, apparently because "state" (without quotation marks) was to be taken as referring to the "form" or "organ" of fructification, sexual ("perfect") or asexual ("imperfect");

(iv) and the priority and broad applicability of the names of genera and species was expressed by vesting "precedence" in "the first valid name or epithet applied to the perfect state ... that which bears asci ... etc."

Gone was the explicit distinction (emphasized in earlier versions of the Article) between giving a name to the "state containing the form which it has been agreed to call the perfect form" and applying it to the species, though this distinction is the continuing intent of the Rule.

The present version of the Article, which came into being in the Edinburgh Code (1966, Art. 59), expresses the same intention by stating that "the correct name of all states ... is the earliest legitimate name typified by the perfect state ... which is characterized by the presence of asci ... etc." Thus, in the phrasing of the Article since its beginning, there has been a clear attempt to restrict "perfect" to meaning "sexual". And, at least since the Stockholm Code (1952), "form" or "organ" or "fructification" could be substituted for "state" in most passages. Yet there remains, even in the current version, reference to "the name for a perfect state" when what is intended is not the name for a sexual organ but for the fungus as a whole.

Some see no incongruity in accepting "perfect state" as meaning "sexual organ" at the same time as "the name for a perfect state" is taken as meaning "the name for a species". To these mycologists, the latter pair of synonyms is merely the expression of the convention imposed by Art. 59: the name for the perfect state (i.e., typified by the sexual organ) is to be taken as the name for the species. To others, the only way to understand a statement such as "the name for a perfect state" is to view "perfect" as "complete to the point of sexual achievement", the sexual fructification as the perfecting or completing form, while "state" is the condition of the fungus. D. Malloch (in litt. 1976), a proponent of this interpretation, has proposed the following definitions to the I.M.A. Subcommittee on Art. 59:

> PERFECT STATE: the complete mode of existence of a fungus, made complete through sexual maturity.
>
> IMPERFECT STATE: the incomplete mode of existence of a fungus, made incomplete through the absence of sexual reproduction.

Hence, the name "for a perfect state" is, to Malloch et al., the name for "the species in its perfect or complete life cycle". And this is most certainly the intent of Art. 59.

To us, it seems that some terms evolve through expansion and restriction to the point where their usefulness becomes questionable. Therefore, we welcome the terms coined by Hennebert (Hennebert & Weresub 1977, reprinted as Chap. 3 of this book) to replace "perfect state" in what has been shown to be its several meanings, and propose to adopt the new terms along with the term resurrected by Donk (1960b) for self-repeating forms. These terms, holomorphosis, teleomorphosis and anamorphosis, return us to the directness of the first Article (Brussels Code 1912) and enable us to express its operation within the type method in unequivocal terms. Since a holomorphosis is a fungus "as a whole, in all its facets, forms and potentialities", it is the ultimate unit of a taxon of Fungi Perfecti. The name of such a taxon, according to

Art. 59, is typified by the sexual form or organ of reproduction; and this sexual form is termed the teleomorphosis. We are thus able to distinguish between the nomenclatural type that determines the application of the name and the ultimate unit of the taxon to which that name is applied, a fundamental distinction in the botanical system of nomenclature (wherein a name applies to a taxon of whole plants, although the type may be a mere fragment of the whole). It also becomes clear through our use of anamorphosis (for the asexual diasporic form) that, in the anatomical system of nomenclature, no distinction exists between the type and the ultimate unit of the taxon to which the name so typified is applied: a form-species is monomorphic, its name typified by an anamorph and applied in accordance with that anamorph to similar anamorphs, and to them alone.

Now having achieved this clarity of expression, we must ask whether it actually reflects our present understanding of pleomorphism. Here we are, spending all this time attempting to link up anamorphoses with teleomorphoses in order to understand the holomorphic pleomorphic fungus, and at the same time we continue to tolerate a sharp nomenclatural distinction between the fungi we classify as holomorphic taxa and those we place in form-taxa. Furthermore, we have yet to solve one of the problems that disturbed the Tulasnes (and was discussed by Hennebert 1971), that of classifying and naming autonomous fungi that seem to be wholly anamorphic. Nevertheless, while recognizing the existence of these unresolved problems, we must not lose sight of what our present system does achieve.

Undoubtedly, it is taxonomically unreasonable to classify, as Fungi Imperfecti, anamorphs of known ascomycetous or basidiomycetous affinity. But surely, as soon as affinities are clear -- as in the case of rust fungi -- a form-taxon can be accommodated among its relatives. A form-genus such as *Uredo* is accepted as a member of the Uredinales Imperfectae, even the Pucciniaceae Imperfectae, long before the form-species in *Uredo* is shown to be affiliated with a known teleomorph. *Papulaspora s.l.* is a form-genus too heterogeneous to be placed anywhere except in the Fungi Imperfecti; but *Papulaspora s.s.* is apparently (Weresub & LeClair 1971) classifiable in the Melanosporaceae Imperfectae. The problem of classifying the anamorphic fungi among teleomorphic relatives is one that Fries was able to solve in dealing with many pleomorphic fungi. Most of our current form-genera can even now be grouped at least as Ascomycetes or Basidiomycetes Imperfectae. And classification at lower levels in the taxonomic hierarchy will become more practicable with every addition to our understanding of the fungi involved. We trust that the time will come when our grasp of the morphology, biochemistry and genetics of all fungi will enable us to classify all anamorphic fungi botanically, as we do uredinaceous anamorphs. Then we will be able to dispense with a pseudo-class such as Fungi Imperfecti (whose pseudonym, Deuteromycetes, attempts to disguise its status as a pseudo-class).

Meanwhile, illogical as it may appear to be, the sharp distinction between names for anamorphs and names for holomorphs does indeed reflect our present adherence to the Tulasne 'doctrine' of pleomorphy. There may still be a few of us who remain as hesitant as the Tulasnes to admit that any fungus can be 'imperfect', because the term bears a connotation of blemish and deformity. All of us are plagued, as the Tulasnes were, by the difficulty of discovering the affiliation of all anamorphs with teleomorphs. Yet, our nomenclatural system demonstrates that, as the Tulasnes felt a century ago, and zoologists (Mayr 1963:28) feel now, most of us

agree that the appropriate way to treat asexual forms is as incomplete, potentially 'perfectable', restricting the term and concept of 'species', and botanical nomenclature, to sexual organisms.

It may be that some individual anamorphs, as well as some pleo-anamorphic fungi, have achieved full autonomy, independent of a teleomorph. But we cannot yet be sure that any particular anamorphic fungus has indeed reached that kind of total independence. The time has not yet come, therefore, when any fungus known only in its anamorphic phase, whether mono- or pleo-anamorphic, should be treated as a species within the botanical system of nomenclature. For practical reasons, we maintain our historic right to provide separate binary names for individual anamorphs even when we know (or suspect) them to be merely portions of a single fungus. But at the same time, we continue to emphasize the anatomical character of the pseudo-species that carry these binary names. It is this emphasis that transforms the biological incongruity of anatomical nomenclature into a tool of our botanical nomenclature. It serves as a strong incentive to prove the affiliation of anamorphs with a teleomorph, when Art. 59 keeps reminding us that, until we do, the names we use are not holomorphic names and do not cover complete fungi. In order that no fungus may be left dismembered, the nomenclature of pleomorphic non-lichenized Ascomycetes and Basidiomycetes continues to abide by the teleomorphic typification of holomorphic names. And that is as far as our present understanding of pleomorphism allows us to go.

The utility of the terms anamorph, teleomorph *and* holomorph, *introduced by Hennebert & Weresub (1977) was so self-evident that the Conference adopted them at the outset. Since they are accordingly liberally sprinkled through the remaining chapters of this book, usually without explanation, I felt it would be wise to give the full text of the paper in which they were proposed, as an appropriate preliminary to their full scale adoption. The text is reproduced from Mycotaxon 6:207-211, by kind permission of the authors and the publishers, in the Chapter which follows.....*

3
Terms for States and Forms of Fungi, Their Names and Types

G.L. Hennebert & L.K. Weresub

In analyzing the nomenclature of pleomorphic imperfecti fungi, Hennebert (1971) proposed the term anatomical to contrast with botanical for denoting the different systems of naming taxa of different kinds. An attempt to extend his analysis to the nomenclature of all perfect and imperfect fungi has revealed the usefulness of certain other terms, as will be seen below.

Obviously, what is called the botanical system of nomenclature is the primary system of the International Code of Botanical Nomenclature (ICBN), with botanical names applied to botanical taxa. In the context of this analysis, what is significant in the botanical system is that the ultimate unit of every botanical taxon is an "individual plant" (Art. 2, ICBN 1972). And an individual plant or organism is an organism as a whole, in all its facets, forms and potentialities, latent or expressed. For the purpose of this discussion, we shall refer to a whole organism as a holomorph (from Gk ολος: holos -- entire).

It is holomorphs that are grouped in botanical taxa, to which botanical names apply. These names are required by the ICBN to be based on nomenclatural types, but the type of a botanical name is not necessarily a holomorph. A nomenclatural type (Art. 7) is "any constituent element ... not necessarily the most typical or representative". In the case of the name of a species, the type specimen is not necessarily a complete organism, not necessarily representing all its forms or all phases of its life cycle, nor even its most typical or characteristic parts. It may be an organism in a state of reproduction or a phase of vegetative growth, a specimen complete or incomplete, fertile or sterile, sexual or asexual. Although "the application of names of taxonomic groups is determined by means of nomenclatural types" (Principle II), there is no intention to restrict the application of a botanical name to whatever part, form, organ or state of an organism is represented on the type specimen. The name, however typified, covers a taxon of complete organisms that make up the species, each of them similar to the individual organism that is represented, perhaps in the whole but probably only in part, by the type specimen.

The system of nomenclature of plants is a botanical system to the extent that holomorphs are the ultimate units of botanical taxa, to which botanical names are given. It is, without qualification, the system of naming non-fossil Cormophytes and Algae, so-called 'lower' fungi (Myxomycota, Mastigomycotina and Zygomycotina: see Ainsworth et al. 1971), as well as lichen-forming Ascomycetes and Basidiomycetes.

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As an example, we may take *Mucor mucedo* Fres., a species described as sporangial and therefore based on the sporangial state of the fungus. Its name is not thereby restricted in application to this state alone. The name covers the whole organism -- the holomorph -- and all organisms judged similar enough to be conspecific, even if their relationship is established on the basis of characters not seen in the type material. When Brefeld later discovered zygospores, a potentiality of the fungus originally unknown, the newly discovered form was automatically covered by the original name by virtue of its botanical application. Neither a new name or a new type was required, no more than an amplification of the known characters of the fungus species, under the botanical name typified by a sporangial state. This is the botanical system without qualification.

The botanical system is also -- but with qualification -- the system for naming Ascomycetes and Basidiomycetes that are not lichen-forming. That these fungi receive names of botanical application is clear in Art. 59 (ICBN 1972), where their names are described as covering "all states which are states of any one species," i.e., holomorphs. But this Article makes a specification regarding the typification of these names. Unlike the type specimen of the botanical name of a holomorphic 'lower' fungus (which may bear any state or form of it), the type specimen of the name of a non-lichenized Ascomycete or Basidiomycete is required to bear evidence of sexuality if the name is to have botanical application to the holomorphic fungus. Art. 59 rules that "the ... name of all states which are states of any one species is the ... name typified by the perfect state ... which is characterized by the presence of asci ... basidia ..." etc. This characterizing form that is involved in producing meiotic diaspores may be termed the teleomorph (from Gk τελεος: teleos -- having perfect achievement, being complete, adult): in Ascomycetes, an ascocarp or its equivalent, at maturity producing asci and ascospores, in Basidiomycetes, a basidiocarp or its equivalent, at maturity producing basidia and basidiospores. Hence, for an autonomous non-lichenized Ascomycete or Basidiomycete to qualify for a botanical name, teleomorphic material must be used to typify that name.

But Art. 59 also provides for the separate naming of these fungi in their asexual state. The Article makes a distinction between the nomenclature of Ascomycetes and Basidiomycetes which qualify for botanical names by virtue of their teleomorphic expression, and the naming of their asexual states and of autonomous Fungi Imperfecti, for which a non-botanical system of nomenclature is in use. This is the system referred to by Donk (1960a) as conventional and by Hennebert (1971) as anatomical. Donk (1960b), in discussing the conventional system further, reintroduced the useful term anamorphosis for the imperfect state, a term we shall proceed to use here for the asexual, mitotic, diasporic expression of a fungus, the form basic to the anatomical scheme.

Anatomical names are applied to anatomical categories or pseudo-taxa (Donk 1960a) whose members are parts of the anatomy of organisms instead of holomorphic organisms; i.e., the ultimate unit of any anatomical taxon is a specified portion, form, or organ of an "individual plant" rather than the individual plant itself.

Thus, it is particular morphs, not holomorphs, that are grouped in anatomical taxa, to which anatomical names apply. These names, like botanical names, are required by the ICBN to be based on nomenclatural types. But in the case of the name of an anatomical species, application is not only determined by, but also restricted to, whatever part, form, state or organ is

represented on the type specimen. In other words, typification and application of anatomical names coincide: the type is the unique morph that is also the ultimate unit of the anatomical taxon.

In the anatomical system governing form- and organ-genera of fossil plants (Art. 3, Note 1), the basis of a taxon is a particular kind of form or organ found in a fossil fragment; and the name is to be applied only to similar forms or organs, not to the holomorphic plant that may eventually be reconstituted from various fragments. In the form-taxa of imperfect fungi (Art. 59), the ultimate unit is a particular kind of anamorph; and the name (referring "only to the state represented by its type") is to be applied only to similar anamorphs; it is not to be applied to the holomorph that is already known -- or eventually discovered -- to include this anamorph, nor is it to be applied to other kinds of anamorphs. As already understood by Hughes (1953), anatomical names -- by definition, typification and application -- are monomorphic (Hennebert 1971).

It is by long-standing convention that these morphs of fossils and of certain fungi are treated in an anatomical system of classification and nomenclature. But if anamorphs of non-lichenized Ascomycetes and Basidiomycetes are conventionally assigned anatomical names, should not the anatomical system be extended to cover also the names based on their teleomorphs? Certainly, if application of a name based on a teleomorph were restricted to this one sexual anatomical part of a fungus, while names based on anamorphs were restricted to single asexual forms, the several names for the same pleomorphic fungus could exist side-by-side without competing for priority. But then, the holomorphic fungus would be denied a botanical name.

Mycological legislators decided in favor of botanical names. In the Brussels Code of 1912, the first special rules for naming fungi established the principle that basing a name on a teleomorph makes it applicable in the botanical sense to a holomorphic fungus. Under Art. 59, the type need not be confined to the teleomorph alone, though it must include it; and the name is not restricted in application to that sexual segment of the fungus, though it undoubtedly covers it. On the contrary, although the teleomorph is a necessary component, the type may include any number of anamorphs as well; and although the name covers whatever morphs are represented in the type, it applies automatically to the holomorph in all its forms, present or not on the type specimen, and including whatever is known or remains to be discovered about the whole organism. Such a name is botanical in its full sense, applied in the same way as a name for so-called 'lower' fungi and lichen-forming Ascomycetes and Basidiomycetes. The fundamental difference between their nomenclature and that of non-lichenized Ascomycetes and Basidiomycetes is that the name of the fungi in the latter groups, when based only on anamorphs, is excluded by convention from botanical status*.

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* In practical terms, it means that, if the type of a name for non-lichenized Ascomycetes or Basidiomycetes includes the teleomorph, the name is botanical and covers the whole fungus. If, on the other hand, the type does not include the teleomorph, the name is anatomical and restricted in application to the form represented by its type.

The Code is concerned with taxa of two kinds and consequently names of two kinds, botanical and anatomical. For most plants and fungi, the system of nomenclature is botanical. Only in the case of autonomous Fungi Imperfecti (Deuteromycetes), the mitotic states of non-lichenized Ascomycetes and Basidiomycetes, and the organ of fossil plants, is the system of

nomenclature anatomical.

In the case of Ascomycetes and Basidiomycetes that are not lichen-forming, one might say that the system is "botanico-anatomical," being jointly botanical (for the entire fungus) and anatomical (for the non-meiotic state of the fungus). This kind of botanico-anatomical system of nomenclature is not at all the same system as that formulated under the same name by Hennebert (1971: 215) for imperfect fungi pleomorphic in themselves. Behind that proposal was an attempt to provide the entire imperfect phase of a fungus with a binary name of botanical effect, while retaining an anatomical monomorphic restriction for names of form-genera, which could thus serve also as terms designating monomorphic states of botanical holomorphic taxa. The relative complexity of this approach to the nomenclature of pleomorphic imperfect fungi (both autonomous and correlated) seems to us now to provide little advantage over the simplicity of the monomorphic anatomical system for form-species as well as form genera.

In summary: as ruled by Article 59, the system of nomenclature for non-lichenized Ascomycetes and Basidiomycetes consists in the co-existence of two distinct systems, the one for taxa of holomorphic fungi and therefore botanical, the other for form-taxa of anamorphs of fungi, treated as anatomical.

All botanical names are *nomina holomorphosium*, applying to organisms as whole beings in all their known or unknown expressions and potentialities. *Nomina holomorphosium* are normally typified by any constituent diagnosable element of the taxon (Art. 7), whether teleomorphic, anamorphic or combining all elements. This is the unqualified botanical system of nomenclature as it applies to plants, 'lower' fungi and lichen-forming 'higher' fungi. In non-lichenized Ascomycetes and Basidiomycetes, *nomina holomorphosium* (botanical names), applicable to holomorphs, are typified at the very least by their teleomorph, whereas names typified by anamorphs alone are *nomina anamorphosium* (anatomical names), and their application is restricted to the single anamorph represented by their type. Anatomical *nomina teleomorphosium* do not exist under our present Code, because a sexual form does not bear a name separate from the name of the holomorphic fungus.

Finally, a word about the Code's ruling requiring the co-existence of a *nomen holomorphosis* and *nomina anamorphosium* for the same Ascomycete or Basidiomycete. As Donk (1960b: 172) pointed out, if a choice has to be made between them, *nomina anamorphosium* automatically become *nomina rejicienda*, giving way to the priority of the *nomen holomorphosis*. Under Art. 59, holomorphic names, being botanical, are priorable; anamorphic names, being anatomical, are unpriorable except within the narrow limits of typification by similar anamorphs.

It is our contention that the terms used above bring into sharper focus the nomenclature of fungi as regulated by ICBN and its Art. 59. Their adoption can turn discussion away from arguments about the meaning of long familiar and no longer uniformly understood terms to a concentration on basic principles.

Having established a terminology in which the nomenclatural problems of the whole fungus might more easily be discussed, it seemed appropriate to broach some of those very nomenclatural problems.....

4
Cross-Reference Names for Pleomorphic Fungi

J.W. Carmichael

Many of the higher fungi can propagate themselves indefinitely by mycelium and conidia. For many species, the conidial state or anamorph is the one usually encountered, and the sexual state or teleomorph is rarely seen. Thus, we are forced to have two different systems of classification in order to be able to identify these fungi in whatever state we find them. First, there is the traditional taxonomic classification, based mostly on the characters of the teleomorph, where the species are grouped into genera and families of the Ascomycotina and Basidiomycotina. Second, there is an additional classification based solely on the morphology of the conidial or other anamorphs. Species with similar conidia are placed in the same form-genus for ease of identification. However, these form-genera are not included in the families of the Ascomycotina and Basidiomycotina. They are kept separate in a group called the Deuteromycotina or Fungi Imperfecti.

It is a basic principle of biological classification that each taxon is a member of only one taxon of the next higher rank. When we classify the anamorph and teleomorph of a single species in two different genera, we violate this principle. As a consequence, we have problems with the nomenclatural principle that each species should have only one valid name. The history of these problems, and three different approaches to solving them, were presented in much detail at the first Kananaskis conference by Hennebert (1971). More recent discussions will be found in Kendrick & Carmichael (1973), Weresub, Malloch & Pirozynski (1974), Sigler & Carmichael (1976), and Hennebert & Weresub (1977 and Chap. 3). I will concentrate here on a single proposal for the use of cross-reference names. The easiest way to outline the proposal is as a set of four rules.

Rule 1- There is only one valid Linnaean binomial for each species.

Rule 2- The first validly published name after the starting point has priority. Exception- For the higher fungi only, the first validly published name for the teleomorph takes precedence over any names published for anamorphs.

Rule 3- Anamorphs of species for which there is an existing valid binomial are referred to by cross-reference names with the format "[form-genus name] state of [Linnaean binomial]." For example: *Monilia* state of *Neurospora sitophila*. Since the name includes both the form-genus for the particular state referred to, and also the binomial for the whole species, it is called a cross-reference name. For indexing purposes, "state of" (or its equivalent in other languages) is replaced by the abbreviation "stat." (Latin - status). An anamorph may

then appear in alphabetic order both under its form-genus name and under the binomial for the species. For example: *Monilia* stat. *Neurospora sitophila* and *Neurospora sitophila* stat. *Monilia*. Regardless of the order, the binomial is left in the nominative to avoid complexity.

Rule 4- Each form genus is based on only one type of anamorph. This anamorph must be present in the type specimen of the type species of the form-genus.

It follows from rules 1 to 4 that where an imperfect species produces two or more types of conidia (or other anamorphs), the earliest valid name for any of the types has priority for that species. The other types of conidia may be indicated by cross-reference names. For example: the *Echinobotryum* state of *Cephalotrichum stemonitis*. This is so even if one anamorph is a Hyphomycete and the other is a Coelomycete. For example: the *Scytalidium* state of *Hendersonula toruloidea*.

The rules seem logical and fairly simple. So why has it taken so long to arrive at them, and why do some people still not accept them? The delay is due partly to conservatism on the part of mycologists, and partly to a number of problems not yet mentioned.

The first problem concerns the specific identity of two different states. Does the cross-referenced anamorph really belong to the same species as the one referred to by the binomial? This is simply the problem of confirming a species identification, but it is obviously more difficult when two different states are involved.

The second problem is that cross-reference names have no separate date, author, or type specimen. The cross-referenced state may or may not be present on the type specimen for the binomial. This means that, to establish a new form genus, it is always necessary to propose a binomial that is typified by a specimen showing the described state. Then, if the type species already has a binomial based on a different state, the newly proposed binomial may be cited as a synonym of the appropriate cross-reference name. Synonymy under cross-reference names is always facultative rather than obligate, since cross-reference names do not have types of their own.

A third problem concerns the definition of the terms "state" and "type" (as used in rules 3 and 4). This seems to me to be a strictly practical problem. We can recognize as states or types whatever it seems useful to have names for. I see no good reason for rejecting form-genera based on spermatia, sclerotia or specialized hyphae, as long as the structures are distinctive enough to permit species identification.

A fourth problem is that cross-reference names are cumbersome. However, they are undoubtedly less cumbersome in the long run than having two or more independent binomials for each pleomorphic species.

DIALOGUE FOLLOWING DR. CARMICHAEL'S PAPER

HENNEBERT: The first point is that we can carry on our discussion using the new terms: *Holomorph* for the entire fungus, however constituted (in extant terminology, this might actually be either a 'perfect species' or an 'imperfect species'). *Teleomorph* for the

sexual fructification. *Anamorph* for the asexual or conidial fructification (we know that parasexuality can occur in anamorphs). The holomorph may include a teleomorph and one or several anamorphs, or anamorphs only.

The second point concerns the reformulation of those parts of the Code referring to fungi and their pleomorphism. (1) The basic principle underlying Article 59 -- the existence of parallel systems of nomenclature for teleomorphs and anamorphs -- is accepted. (2) The two systems are entirely separate, and no synonymy is possible between them, since the application of the names of anamorphs is based strictly on what is present on the type material. (3) The application of separate binomials to the different morphs of a pleomorphic fungus is accepted as inevitable. These principles are incorporated in a proposal for the modification of Article 59 emerging from the deliberations of the Nomenclature Subcommittee at the Mycological Congress, Tampa.

The third point concerns the nomenclature of holomorphs completing their life cycle in the anamorphic condition (what we have always called imperfect fungi). Three possible systems were outlined at Kananaskis-I, of which two have now been rejected, at least implicitly, and the third accepted. The 'botanical' system has been rejected because its application would mean that form specific epithets and form generic names would automatically be regarded as the names of proper species and genera, and therefore applicable to all parts of the fungus. This would allow full synonymization between 'form' and 'proper' epithets, and would logically lead to the abandonment of Article 59.

The 'botanico-anatomical' system has also been rejected because it, too, proposed a wider application of anamorphic names than is now permissible.

The only system remaining is the 'anatomical system'. This permits the provision of a binomial for each morph of a pleomorphic fungus, but gives no indication of the genetic connection between the different morphs.

Dr. Carmichael's system might best be called a refined anatomical system. Why refined? In a purely anatomical system every anamorph of the same fungus receives a binomial based on a type in which that anamorph is represented. These names are used in parallel with no indication of the relationship between them. Dr. Carmichael has proposed that, where the connection is known, only one of those binomials be used -- the earliest applied to any one of them. When it is desired to refer to any anamorph other than that providing the binomial, the form generic name of the anamorph in question would be cited, in a combination with the accepted binomial.

CARMICHAEL: Cross-reference names were first used systematically by M.B. Ellis and S.J. Hughes (beginning in 1958) for referring to anamorphs whose teleomorph is known. My proposal is that we continue this practice and extend the system to apply to the different anamorphs of species with no known teleomorphs. The Code at present allows as many binomials for a species as there are recognized anamorphic states. A system of cross-reference names would allow us to designate particular anamorphs without using more than one binomial for a single species.

WERESUB: Do you intend that this be brought forth as a ruling or as a recommendation?

CARMICHAEL: You can't force people to use names they don't want. I have simply developed

this as a logical extension of what many mycologists are currently doing, and provided it with a proper rationale. It is not at present contrary to the rules of botanical nomenclature to use cross-reference names. Rules I leave to your discretion.

PIROZYNSKI: If this became a rule, wouldn't *Sclerotium* have to replace *Botrytis*, since it is an earlier name?

CARMICHAEL: No. *Sclerotium* is not an earlier name for the *Botrytis* state. Form generic names apply to a single state: *Sclerotium* to a sclerotial anamorph, *Botrytis* to a conidial anamorph. If the fungus we call *Botrytis cinerea* had earlier been named *Sclerotium durum*, the proper name in *Botrytis* would be the *Botrytis* form of *Sclerotium durum*. But that doesn't make *Botrytis* a synonym of *Sclerotium:* they are based on forms of different kinds. If the teleomorph is discovered to be a *Botryotinia*, then the anamorphic binomials are abandoned, and you have 'the *Botrytis* form of *Botryotinia fuckeliana*' and 'the *Sclerotium* form of *B. fuckeliana*'.

KENDRICK: What if, in pleomorphic anamorphs, connections are made in different directions; for example, in one case the *Scytalidium* is described first and its *Hendersonula* state discovered later, while in another case the *Hendersonula* is described first, the *Scytalidium* state later on. In one case the citation would be 'the *Hendersonula* state of *Scytalidium x*', in the other, the '*Scytalidium* state of *Hendersonula y*' -- one binomial would be in *Scytalidium*, one in *Hendersonula*. Would that not create confusion and complicate or frustrate attempts at indexing?

CARMICHAEL: No, because in any index each taxon is listed under both the form generic (cross-reference) name and also under the binomial, so they wouldn't become disconnected even in reversed pairings such as those you mentioned. That is the chief purpose in using cross-reference names, to prevent the disconnection that arises when one species has two or more binomials.

WERESUB: Using a binomial as if it were a botanical name while at the same time retaining the un-botanical form-generic name seems to be a rather illogical way of linking the two systems. It seems to me that you must either have a botanical name -- a binomial -- or an anatomical name -- a form genus and an epithet for the form. But when you try to combine the botanical with the anatomical, the mis-match is troublesome.

CARMICHAEL: If we do not know the teleomorph, the best botanical name we can propose has to be in a form-genus. It's all we've got: it's the best we can do. It's not as desirable as a name in a genus that is part of the over-all classification of fungi, but is a compromise necessitated by the nature of the organism, and it doesn't seem unreasonable or improper to me. It seems to me to be what Dr. Hennebert (1971) called a 'Botanico-anatomical' system.

WERESUB: I wonder if Dr. Hennebert, in his botanico-anatomical proposal, anticipated that closely related fungi could be placed in widely different genera, e.g. in Kendrick's example: the anamorphic species *x* placed in *Scytalidium* and the closely related anamorphic species *y* placed in *Hendersonula*. That is a strange botanical treatment.

CARMICHAEL: It's the best we can do, unless we abandon the idea of priority, and I'm not sure what could replace it.

WERESUB: But the principle of priority does not force me to use the earliest binomial no matter what my taxonomic views are. The principle of priority forces me to use the earliest legitimate epithet applicable to the species, and combine it with the earliest legitimate name of the genus that I consider appropriate...a genus whose name is typified by a species I consider to be congeneric with my species. In a purely anatomical scheme of naming anamorphs, priority causes little difficulty. But as soon as the application of a nomen anamorphosis acquires a botanical circumscription, the principle of priority must surely take on its botanical sense as well as its chronological value. If I judge two species to be closely related, I must surely be allowed to put them together in one genus. It seems to me that you must either have a botanical name -- a binary name for a holomorph -- and therefore a botanical sense for the genus; or you have an anatomical name -- a binary name for the anamorph -- and the genus is clearly anatomical. When you mix these concepts, the synthesis is confusing.

HENNEBERT: The botanical system, as I proposed it in 1971 with reference to pleomorphic anamorphic species, would apply the rule of priority in its full sense, botanical and chronological, at both ranks of genera and species. In the botanico-anatomical system, conceived from my interpretation of Dr. S.J. Hughes's usage in 1958, the rule of priority applies only at the specific rank, all epithets given to any of the anamorphs being taken botanically and thus considered synonyms, the earliest available being retained. The generic name remains anatomical. In Dr. Carmichael's system, the rule of priority applies fully only among the epithets given to any one of the anamorphs. These then are synonyms among themselves but not synonymous with epithets given to other anamorphs in the pleomorphic species. Then a sort of rule of anteriority selects the oldest epithet amongst the correct (but not synonymous) epithets of all the anamorphs, resulting -- as in my botanico-anatomical system -- in the retention of the oldest available epithet.

The whole difference lies in how broadly the rule of priority is applied. In Dr. Carmichael's system, the specific epithet is not transferable from one genus to another representing a different anamorph. The epithet remains an anatomical one, tied to its monomorphic type. In the botanico-anatomical system, the epithet is a botanical one, and thus transferable to any one of the genera representing the different anamorphs of the fungus -- for instance, in the case referred to previously, from *Sclerotium* to *Botrytis* or vice versa. In an anatomical system, the epithet *durum*, being based on a sclerotium, has to be tied to a generic named typified by sclerotia. But if we treat that epithet botanically, so that it is available, by way of priority, to the unique binomial given to an entire anamorphic species (comprising all its morphs), as in the botanico-anatomical system, then it can be transferred, for example, to *Botrytis*; and *Botrytis dura* would be the unique binomial for the whole anamorphic species. The same procedure with other anamorphic species would bring all of them together within the same anamorph-genus. The generic name remaining anatomical, attached to its type, for the purpose of the cross-reference names designating the different anamorphs separately, we would have:

Botrytis dura anam. *Botrytis*
Botrytis dura anam. *Sclerotium*
Botrytis dura anam. *Myrioconium*.

WERESUB: Would you allow an arbitrary choice of the generic name?

HENNEBERT: A choice of the generic name on taxonomic or biological grounds has been suggested by Hughes in 1958, and it works. It is also conceivable -- though perhaps not without difficulty -- that the oldest of the correct generic names for the different anamorphs is chosen according to a sort of rule of anteriority. But this would result in bringing together, in one genus such as *Sclerotium*, species having distinct conidial anamorphs, such as *Botrytis*, *Amphobotrys*, *Streptobotrys*, along with species that have no conidial anamorphs at all.

To give you my suggested botanico-anatomical system in a nutshell: the generic name is anatomical and used as such in both the cross-reference name and the binomial, and the specific epithet is botanical.

In Dr. Carmichael's proposal, the epithet is treated as anatomical, and so cannot be transferred out of genera whose names are typified by the same kind of morph Thus, if *Sclerotium durum* has priority over *Botrytis cinerea*, *Sclerotium durum* would have to be used as the combination for the whole anamorphic species; *durum* could not be transferred to *Botrytis*. A related fungus, *Botrytis globosa*, which has no earlier name in *Sclerotium*, would remain in *Botrytis*. In a third example of a related fungus -- I'll use mythical names -- *Botrytis praetermissa* is predated by the binomial for its *Myrioconium* morph as *Myrioconium candidum*; the binomial would have to be *M. candidum*. Thus, in Dr. Carmichael's scheme, we could have *Botrytis* anamorphs listed under unique binomials in three different anamorph-genera. That is the kind of problem that can arise in pleo-anamorphic species. It would be minimized if epithets were transferable, as botanical, to any of the available generic names for the species: in the botanico-anatomical system as conceived by me, the three species would be called *Botrytis dura*, *Botrytis globosa* and *Botrytis candida*.

KENDRICK: Can I perhaps try to put this issue in perspective by outlining the six positions that have been adopted to date by various authorities in the naming of pleomorphic anamorphic species. (1) the binomial is chosen arbitrarily by the author according to which anamorph (the lectomorph) is judged to be the more characteristic, common or conspicuous. Problems arise here because of conflicting interpretations of these concepts. Dr. Hennebert (1967) regarded the chlamydosporic morph of *Chalara (Chalaropsis) punctulata* as more characteristic than the phialidic form. Dr. Nag Raj and I (1975) considered the phialidic morph to be the more taxonomically informative of the two. (2) To get around this particular difficulty we could adopt Wakefield's (1929) proposal that the choice made by the first author to treat the connection be accepted, or (3) we could accept the earliest available binomial given to any of the morphs, as proposed by Carmichael. (4) We could assign both generic and specific epithets according to the rule of priority, as Hennebert suggests. (5) We could allow the application of a separate binomial to each morph: a practice that has been fairly common in the past, even when the connection was known. (6) In some cases, particularly where two different anamorphs are intimately associated, a single binomial, that by definition requires the presence of both anamorphs, has been applied (e.g., *Thielaviopsis*, *Chalaropsis*, *Diheterospora*). This is widely regarded as undesirable, but such names persist, partly because we have not been able to arrive at a consensus on this problem. We may not be able to decide here and now which we want to

adopt, but I think perhaps we can be made aware of all the possible choices, and of their relative advantages.

LUTTRELL: If I might return to a discussion of species for which teleomorphs are known. There is a tendency among mycologists to describe the teleomorph, and then to add, as an afterthought almost, that it has a '*Fusarium*'-like anamorph. This simply avoids the issue. I would like to see it obligatory that authors assign anamorphs to a form-genus, and not leave them in limbo. If they can decide on a genus for the teleomorph, then they should make the effort to do likewise for the anamorph.

This brings up another point. The nomenclature of holomorphs which have teleomorphs submits to the taxonomic decision that the teleomorph is the prime form of the species. This is acceptable. Surely, however, we must learn to make taxonomic decisions in the pleomorphic anamorphs, and not copy out by allowing a nomenclatural rule to pre-empt our taxonomic judgment. Is not nomenclature supposed to serve taxonomy?

KENDRICK: I tend to agree with your basic premise, but what if taxonomic interpretations differ -- they can even be diametrically opposed, as I mentioned earlier?

WERESUB: The rules of nomenclature exist simply to give you some direction on how to express your taxonomic opinion. But they must allow you to express whatever kind of taxonomic opinion you hold, no matter how idiotic that opinion may be. The rules govern nomenclature, not taxonomy.

CARMICHAEL: The rules are meant to ensure that when you have made any particular taxonomic decision, there is then only one correct name for each taxonomic entity. You can only change the name if you change your taxonomic decision. And although the present system allows separate binomials for anamorph(s) and teleomorph, I would prefer that there should be only one valid binomial per holomorph. I have set forth a procedure for achieving this. We have a problem in that real species must be assigned to form genera. We can suggest that form genera are not real genera because one species (in its various anamorphs) can belong to more than one form genus. The problem is to get around this without having more than one binomial. I think the way to do it is by using cross-reference names.

HENNEBERT: The binomial may designate a pleomorphic organism. The cross-reference name must designate a monomorphic state. Stan Hughes based his nomenclature on this important point. Then, of course, there arises the problem of pleomorphic imperfects (anamorphs). In Kananaskis-I, I ignored the existence of Article 59, since teleomorphic names were not involved, and also because Article 59 might remain as it was, be changed or be deleted altogether. So, considering only the anamorphs, I found that there were three ways of treating their nomenclature.

If we treat anamorphic names in a fully botanical sense, we must logically dispose of Article 59. There is no longer any need for two systems of nomenclature, because the botanical anamorphic names must be applicable, where this is dictated by priority, to the holomorphs including teleomorphs.

VON ARX: To me this is a very practical matter: I have *Curvularia lunata* -- a very common and well-known fungus. When it is submitted to our identification service we have to use this name, because no one has actually seen the ascigerous teleomorph -- the connection

was described only once. Many ascomycete names have been incorrectly put forward as being teleomorphs of particular conidial fungi -- when in fact one or other state has simply been a contaminant. There are many such examples, and we will be exposed to many inaccuracies if we insist on using only the name of the teleomorph. We also have a large culture collection, and we find it both convenient and necessary to give all species of *Penicillium* their anamorphic name rather than the teleomorphic name in *Talaromyces*. I cannot use the name *Cochliobolus* when I write a report -- I must use the name of the commonly occurring state -- the conidial anamorph, by which the fungus is generally known. We are not always sure of the connections. For practical reasons I prefer to use a binomial for the conidial fungus, because phytopathologists and people working in biodegradation just do not know or recognize the other name.

HENNEBERT: You have advanced some good practical reasons for choosing an anatomical system. This means that you would prefer to maintain the system sanctioned by Article 59 as has happened up to now. I was speaking from the theoretical basis for names. Perhaps if we approach this question from both theoretical and practical angles, we can meet somewhere.

VON ARX: I know some anamorphs for which an entirely incorrect teleomorph has been proposed. So I prefer to name the fungus I see under the microscope rather than relying on someone else's previous decision, which may have been wrong.

HENNEBERT: That is why I don't use *Botryotinia fuckeliana* much. *Botrytis cinerea* is a complex species -- it probably encompasses more than one genotype -- and we never know when we see *Botrytis cinerea* which *Botryotinia* we are dealing with.

CARMICHAEL: You are coming out in favour of retaining form species. You wish to treat *Curvularia lunata* not as a biological species but as a form species. This is perhaps, like *Botrytis cinerea*, a group of biological species that you cannot at present separate, so you are lumping them under one name, one binomial, which suggests that you have one real species when you actually have more than one. Surely in this situation you should make it clear to your 'customers' that you are dealing with an 'aggregate'?

You also suggest that you can't teach plant pathologists to accept a new nomenclatural system, or even new names. I think this is incorrect: it simply takes time. In medical mycology we have succeeded in weaning the practitioners away from calling yeasts *Monilia* (after 50 years of trying).

KENDRICK: The point is surely that mycologists, who insist on this double system of names, are in a very small minority among the biologists who study the living kingdoms. This make us real odd-balls -- despite all the good reasons we have for being so -- and we might ask ourselves whether we should not perhaps be more compliant to the will of the majority. Other people do have problems fairly similar to those we face, and they deal with them differently.

WERESUB: I understand that the phycologists may be considering accepting a system of anatomical names along the same line as the one we now use, and from which Dr. Carmichael proposes we move away for the sake of the few cases there may be of anamorphic holomorphy.

PIROZYNSKI: We began with three very useful terms, but now we appear to have synthesized an extra one, the 'anamorphic holomorph'. Couldn't we rather say 'anamorphic species' for such apparently autonomous anamorph(s)? The term 'anamorphic holomorphy' may be confusing

because there is always a possibility that a teleomorph will be discovered.

WEBSTER: We never know, of course, whether we have discovered the entire fungus, since there always remains the possibility that further unreported morphs exist. I have thought for a long time that *Aspergillus niger* might not have a teleomorph, but I am prepared to be surprised. I would be delighted if it were shown to have one. This fungus might be heterothallic, and sooner or later someone may put compatible strains together and produce the teleomorph.

KENDRICK: I believe that there exist genuinely anamorphic holomorphs -- fungi which, even in their entirety, do not encompass a teleomorph. I see no reason why some fungi which began life as perfectly ordinary Ascomycetes and Basidiomycetes should not, through the normal processes of evolution, have lost the necessity, and ultimately the ability, to produce teleomorphs. This has happened in other groups of organisms, so why not in the fungi? It may be a long time before we can fully test that hypothesis, but if we do not admit this possibility, then our concept of holomorphs is likely to remain a very theoretical one for most fungi. Even when we do know of a connection between an anamorph and a teleomorph, we may still know only part of the total possible phenotypic expression of the genome.

HENNEBERT: Holomorphs may be monomorphic, dimorphic or polymorphic.

VON ARX: Relatively few cases are polymorphic.

WATLING: In the case of a fungus for which the only morphs known are two anamorphs, we could suggest the term 'dianamorphic'.

KENDRICK: That sounds like a Greek goddess rather than an asexual fungus.

WATLING: It would add a little spice to mycology.

MADELIN: Must we use the term holomorph only in a rather abstract way?

HENNEBERT: The term covers what is implied by the phrase: botanical species; and although we may not know all its parts, we can yet give the totality a name, which, by the provisions of the Botanical Code, is the binomial applied to the teleomorph. But our discussion has been mainly concerned with what we are to call fungi which lack a known teleomorph, but have more than one anamorph. Should a teleomorph turn up, it automatically provides the name for the holomorph. We need to agree on a rational, standardized approach to the naming of fungi which appear to be strictly anamorphic.

WERESUB: We don't normally give binomials to such expressions as spermatial or microconidial states, but people must have the freedom to do that, if they so desire.

LUTTRELL: You are quite right; science is perfectly capable of protecting itself. If such names are useful, they will stick; if not, they will be discarded. Science is self-pruning. I approve of anything that leaves people free to make their own judgement.

MADELIN: But the Code does impose certain limitations on what we can do. For example, the ultimate name of the holomorph must be that of the teleomorph. This prevents us from classifying the higher fungi on the basis of their anamorphs, for which we might be able to make a perfectly good case.

LUTTRELL: Raper made that case. It seemed logical and reasonable in *Aspergillus* and *Penicillium*. We might be able to tolerate a dual system, as long as the name is tied to one type. But we must accept some standardization if we are to avoid chaos.

MADELIN: What if teleomorphs in the same genus, for example, *Mycosphaerella*, have anamorphs from different form genera. The holomorphs would have to be called *Mycosphaerella* even if their anamorphic components were quite different. Unless you say "This teleomorph plus this anamorph equals one thing; this teleomorph plus that anamorph equals something else", the current system certainly seems to entrench the supremacy of the teleomorph in the classification, and flies in the fact of much that has been said here at Kananaskis-II.

KENDRICK: This problem has arisen, and has been acknowledged, before. This was when it was realized that different *Ceratocystis* teleomorphs can have very different anamorphs. The same thing happened in *Sclerotinia*. Both of these genera were split up into a number of segregate genera on the basis of their disparate anamorphs. If the anamorph assumed sufficient importance, even the most hardened Ascomycete specialist will probably do something about it.

VON ARX: I think that if we base the classification of ascomycetous teleomorphs on their associated anamorphs, the resulting genera tend to be unnatural. For example, some of the new genera segregated from *Sclerotinia* are less natural than the old *Sclerotinia* sensu lato. This is because some *Sclerotinia* species which produce no anamorph are now placed in a separate genus from other very similar species which produce *Botrytis* anamorphs. In these cases the anamorph rather than the teleomorph appears to have gained the ascendancy. As far as I know, species of *Puccinia* which do not produce uredinia or aecia are not classified in another genus, so I don't see why this should be done in the Sclerotiniaceae. *Mycosphaerella* species include anamorphs belonging to genera such as *Septoria*, *Ramularia*, *Ovularia*, *Cercospora*, *Heterosporium* and *Cladosporium*. Other species do not include anamorphs or only an *Asteromella* spermatial state. Divisions of *Mycosphaerella* into a number of genera characterized by their anamorphs, as proposed by Klebahn (1918) would only result in unnatural taxa. Species delimitation is often not possible on the basis of this character. One example is *Mycosphaerella tassiana*. Most of the isolates form a *Cladosporium* in culture, while isolates from alpine or arctic regions (with a short growing season) form only the teleomorph. *Mycosphaerella allicina* is morphologically similar to *Mycosphaerella tassiana*, but does not include an anamorph. (This species is parasitic on *Lilium philadelphicum* and I have collected it during one of our forays here at Kananaskis.)

WEBSTER: The lack of an anamorph may be due simply to geographical or climatic factors. We have found a form of *Hypocrea rufa* in sand dunes that produces no *Trichoderma* anamorph. We have recognized its similarity to those which do develop the anamorph, and have just called it a 'forma sterilis'. Perhaps a similar approach would resolve the problem in *Sclerotinia*.

MADELIN: It is possible that in this case you may be looking at two strains that may or may not be interfertile. If the sand dune variety of *Hypocrea rufa* is not interfertile with the *Trichoderma*-producing strains, you may (according to one definition) have two physiologically different species, despite the fact that you can't separate the teleomorphs on morphological grounds.

WATLING: This is a common phenomenon in *Coprinus*, and the strains involved can only be considered incipient species. But the present system of classification is based on the

morphology of the teleomorph; if we abandon this particular set of characters, we are going to get into an awful lot of trouble.

KENDRICK: In the *Hypocrea* and the *Sclerotinia* species some of the morphological characters on which we usually make taxonomic decisions are missing. Is this perhaps a little like the case of *Ophiostoma* and *Europhium*, the latter being little more than a neckless, non-ostiolate version of the former? Some characters have been changed or lost, but that doesn't prevent us from using the rest to recognize basic relationships.

At this point the meeting was brought back to the topic of the terms, and quickly gave unanimous approval for the use of anamorph, teleomorph *and* holomorph *in describing the various expressions of fungal genomes. The terms* ascoma, basidioma *and* conidioma *also received a unanimous stamp of approval. The meeting also sought for a more precise term to replace the terms 'connected' or 'correlated'. Various suggestions included 'affiliated,' 'linked,' 'integrated,' 'belonging to,' 'interrelated,' but none was found that could be wholeheartedly endorsed by the gathering. The decision was to retain the original terms, each possibly prefaced by the word 'genetically.' The meeting suggested that although all the commonly used words had some built-in problems arising from multiple use, it was not necessary to coin another new term to express the linkage between morphs of the same fungus, and that in each language usage would probably prevail over scientific precision. Following this surprisingly sensible decision, Dr. Kendrick suggested that perhaps the discussion had come full circle and that those members of the Conference with the greatest nomenclatural experience and expertise (Drs. Weresub, Hennebert, and Carmichael) should form a small committee to deliberate and produce a distillate of their ideas for the Conference as a whole. Dr. Weresub suggested that the idea of a Committee was useful only for the committee itself, since -- when complex problems are involved -- only the Committee comes out of it with a full understanding of the problems, their report necessarily missing the evolutionary process that led to their understanding. Dr. Kendrick noted that he had attended some of the nomenclature sessions at the recent Mycological Congress in Florida, and thus appreciated that there was an inevitable loss of information in the kind of procedure he had proposed, but said that the other members of the Conference, not to mention the readers of this book, would be grateful for any enlightenment the nomenclaturists could provide. Ultimately a 'non-committee' was constituted involving various permutations and combinations of the three people mentioned above, and their report appears as Chapter 27 of this book.*

Now the preliminaries were almost over, and the Conference was ready to get down to cases; but because of my longstanding commitment to clear, unequivocal terminology as an aid to communication among taxonomists, I have here interjected a terminological supplement, prepared with the help of my colleague, Dr. Nag Raj. We have tried to extend the theme of clarification into the morphology of the anamorph.....

5
Morphological Terms in Fungi Imperfecti

B. Kendrick & T.R. Nag Raj

In recent years the attention of many students of the Fungi Imperfecti has been sharply, almost exclusively, focussed on developmental phenomena. This trend was laudable in that it led to the accretion of much valuable new knowledge. But, as has been explained elsewhere (Kendrick 1978), and as may be deduced from Chapters 6 and 7 in this book by Dr. Madelin and Mrs. Wang, we can no longer cling to the fond hope that a new and 'natural' classification, based on developmental features, is just around the corner. Once we have abandoned this illusion, we can turn our attention to a reassessment of the more traditional characters, which have been in eclipse for some time. Morphological criteria are still widely used, and will obviously remain in service for the foreseeable future. On close inspection, some of the terminology involved in describing morphological features can be seen to be remarkably imprecise, or even to some extent misleading. This is becoming a serious problem, because the number of taxa described in the Fungi Imperfecti is growing, inexorably and rapidly, generating a need for more accurate communication. The following remarks represent an attempt at overhauling and refurbishing some old friends so that they may help to fill that need.

THE SPORES OF FUNGI IMPERFECTI

The morphological categories established for mature conidia by Saccardo in the 19th century are still useful. Kendrick & Carmichael (1973) acknowledged this in the arrangement of their illustrations of 566 Hyphomycete genera. And unlike many other mycological terms, the etymology of the names of these categories is relatively accessible. It is not difficult to decipher amerospore (Greek: ameristos = undivided), didymospore (Greek: didymos = twin or double), phragmospore (Greek: phragm = partition), helicospore (Greek: helix = twisted), dictyospore (Greek: diktyon = a net, hence with septation resembling a net), scolecospore (Greek: skolex = a worm), and staurospore (Greek: stauros = a cross, hence with radiating arms).

It was not until it had to be decided, for the purpose of arranging illustrations, when a phragmospore was not a phragmospore but a scolecospore (or vice versa), and whether a given array of protuberances merited the name staurospore or not, that the lack of precision inherent in some of these terms was fully realized.

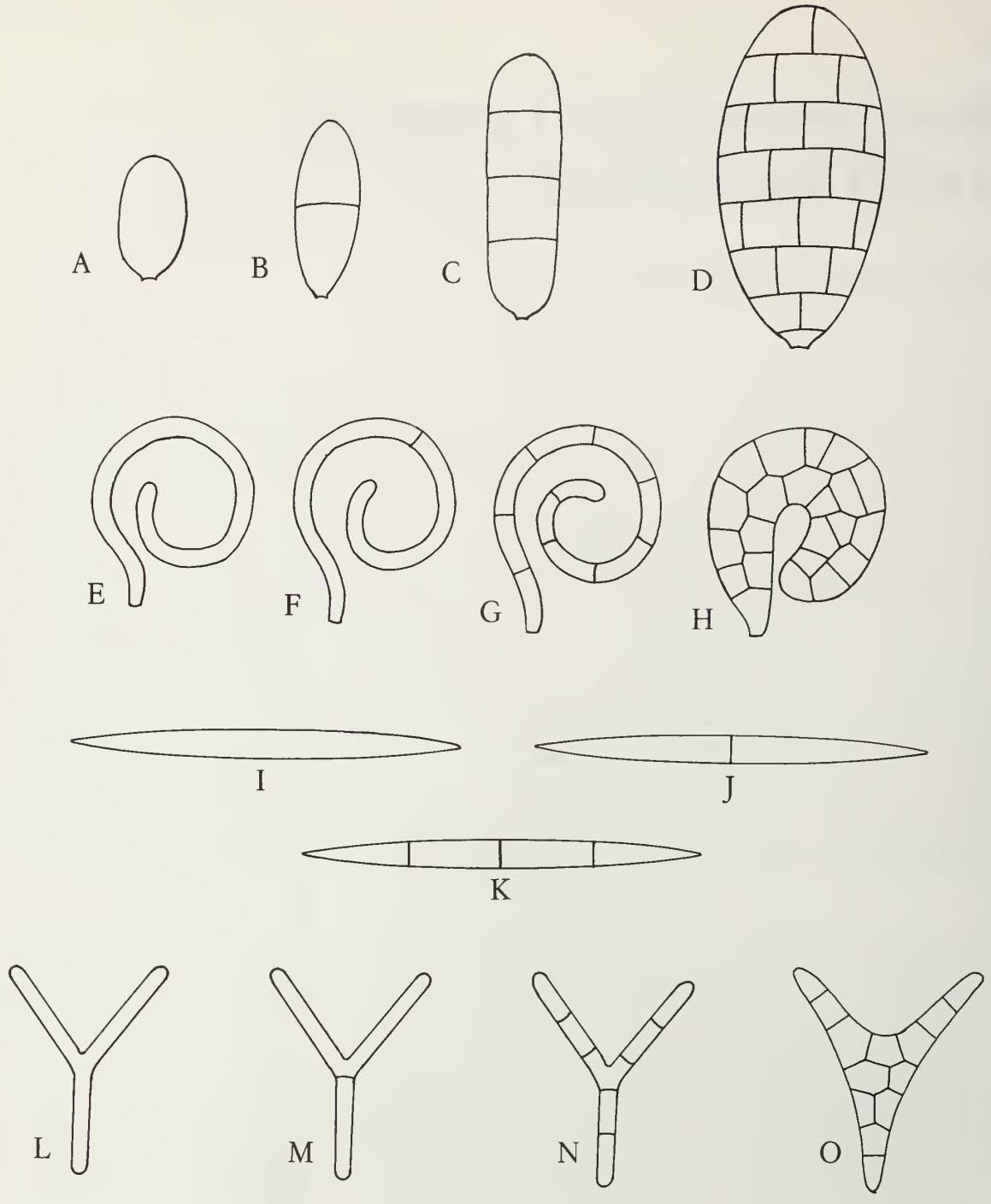

Fig. 5.1 A, amerospore; B, didymospore; C, phragmospore; D, dictyospore; E-H, helicospores which could also be regarded as, respectively, amero-, didymo-, phragmo-, and dictyo-spore; I-K, scolecospores which could be regarded as, respectively, amero-, didymo-, and phragmo-spore; L-O, staurospores which could be regarded as, respectively, amero-, didymo-, phragmo-, and dictyo-spore.

Indeed, if we examine the categories more closely, we detect certain inconsistencies or ambiguities in the logic of the system. It is clearly impossible for an amerospore to be a didymospore, a didymospore to be a phragmospore, or a phragmospore to be a dictyospore (Fig. 5.1 A-D). Yet it is possible for a helicospore to be an amerospore, a didymospore, a phragmospore, or even a dictyospore (most are actually phragmospores) (Fig. 5.1 E-H). It is equally possible for a scolecospore to be an amerospore, a didymospore, or a phragmospore (Fig. 5.1 I-K). It is even possible for a staurospore to be an amerospore, a didymospore, a phragmospore or a dictyospore (Fig. 5.1 L-O). It is all a matter of curvature or proportion.

It appears that there are two character sets harnessed together or superimposed -- that based on *septation* and that based on *shape*, with the latter often gaining the ascendancy. At first glance, it seems that the septal arrangements are always easily distinguishable, while the shapes are potentially confusing. This is almost true. It is very difficult, given only what one can glean from the literature by way of limits for the Saccardoan shapes, to decide when a spore is long enough in relation to its width to be called a scolecospore (which of the illustrations in Fig. 5.2 A-F represent 'true' scolecospores?). Or to decide when protuberances are conspicuous enough or long enough in relation to the body of the spore to confer the title staurospore (Fig. 5.2 G-J).

We hope we have established that the Saccardoan terms give rise to sufficient 'grey areas' to call for some clarification. The first aim of this paper is to supply the requisite demarcations. It must be understood that the limits we shall propose are arbitrary, but it is our intention wherever possible to follow the spirit of the original author in the definitions which follow.

Amerospore -- a non-septate spore with a length/width ratio not exceeding 15:1; if elongated, with only a single axis, and that axis not curved through more than 180°; any protuberances, other than setulae, not more than 1/4 the length of the spore body.

Didymospore -- a spore with 1 septum across the body; with a length/width ratio not exceeding 15:1; if elongated, with only a single axis, and that axis not curved through more than 180°; any protuberances, other than setulae, not more than 1/4 the length of the spore body.

Phragmospore -- a spore subdivided by two to many septa, all transverse; with a length/width ratio not exceeding 15:1; if elongated, with only a single axis, and that axis not curved through more than 180°; any protuberances, other than setulae, not more than 1/4 the length of the spore body.

Dictyospore -- a spore subdivided by *intersecting* septa in more than one plane; with a length/width ratio not exceeding 15:1; if elongated, with only a single axis, and that axis not curved through more than 180°; any protuberances, other than setulae, not more than 1/4 the length of the spore body.

Helicospore -- a spore with or without septa; with a single, usually elongated, axis which is curved through at least 180°, but may describe one or more complete rotations, in two or in three dimensions; any protuberances, other than setulae, not more than 1/4 the length of the spore body.

Scolecospore -- a spore with or without septa; with a length/width ratio exceeding 15:1; with a single axis, not curved through more than 180°; any protuberances, other than setulae, not more than 1/4 the length of the spore body.

Staurospore -- a spore with or without septa; with more than one recognizable axis; axes not curved through more than 180°; protuberances, other than setulae, present and exceeding 1/4 the length of the spore body.

When one has adequately discriminated and described the species in a genus, it is usual to provide a key to help the non-specialist identify them. The definitions given above are designed not simply to be mutually exclusive, but also to stand on their own. Thus each contains several exclusion clauses which, though necessary, may seem rather repetitive, and to the uninitiated may serve to obscure the positive diagnostic features. Accordingly we have adopted the traditional expedient of supplying a key. This should enable even inexperienced students to decide what morphological category any spore belongs to.

1 Spore axis curved through more than 180° ..... Helicospore
1 Spore axis not curved through more than 180° 2
  2 Spore with more than one axis; protuberance(s), other than setulae, present and more than 1/4 the length of the spore body ..... Staurospore
  2 Spore with only one axis; any protuberances, other than setulae, if present, not more than 1/4 the length of the spore body 3
3 Length/width ratio of spore body exceeding 15:1 ..... Scolecospore
3 Length/width ratio of spore body less than 15:1 4
  4 Spore lacking septa ..... Amerospore
  4 Spore with 1 or more septa 5
5 Spore with 1 septum ..... Didymospore
5 Spore with more than 1 septum 6
  6 Spore with only transverse septa ..... Phragmospore
  6 Spore body subdivided by intersecting septa in more than one plane ..... Dictyospore

The spore axis is a line that passes through the centre of the spore from one extremity to the other (in the case of tetraradiate and other spores classified as staurospores, there are more than two recognizable extremities and, accordingly, more than one axis). The 'minimal' helicospore is one in which the axis is curved sufficiently that, if extrapolated, it will intersect with itself when viewed from the side (Fig. 5.2 K). We do *not* regard as a helicospore any curved spore whose axis does not meet this requirement, e.g., Fig. 5.2 L. Our definition aims at following current usage as closely as possible in setting a lower limit of curvature. Most helicospores are very obviously, and often repeatedly, coiled in two or three dimensions.

The requirement for the septa of dictyospores to intersect is necessitated by such things as the configuration of many helicospores. Although septa may be transverse with relation to the spore axis, if the spore is viewed as a whole, septa certainly occur in more than one plane, as do those found in many staurospores. Dictyospores are usually spores of some substance, and many intersecting septa can usually be found with ease. However, for the record,

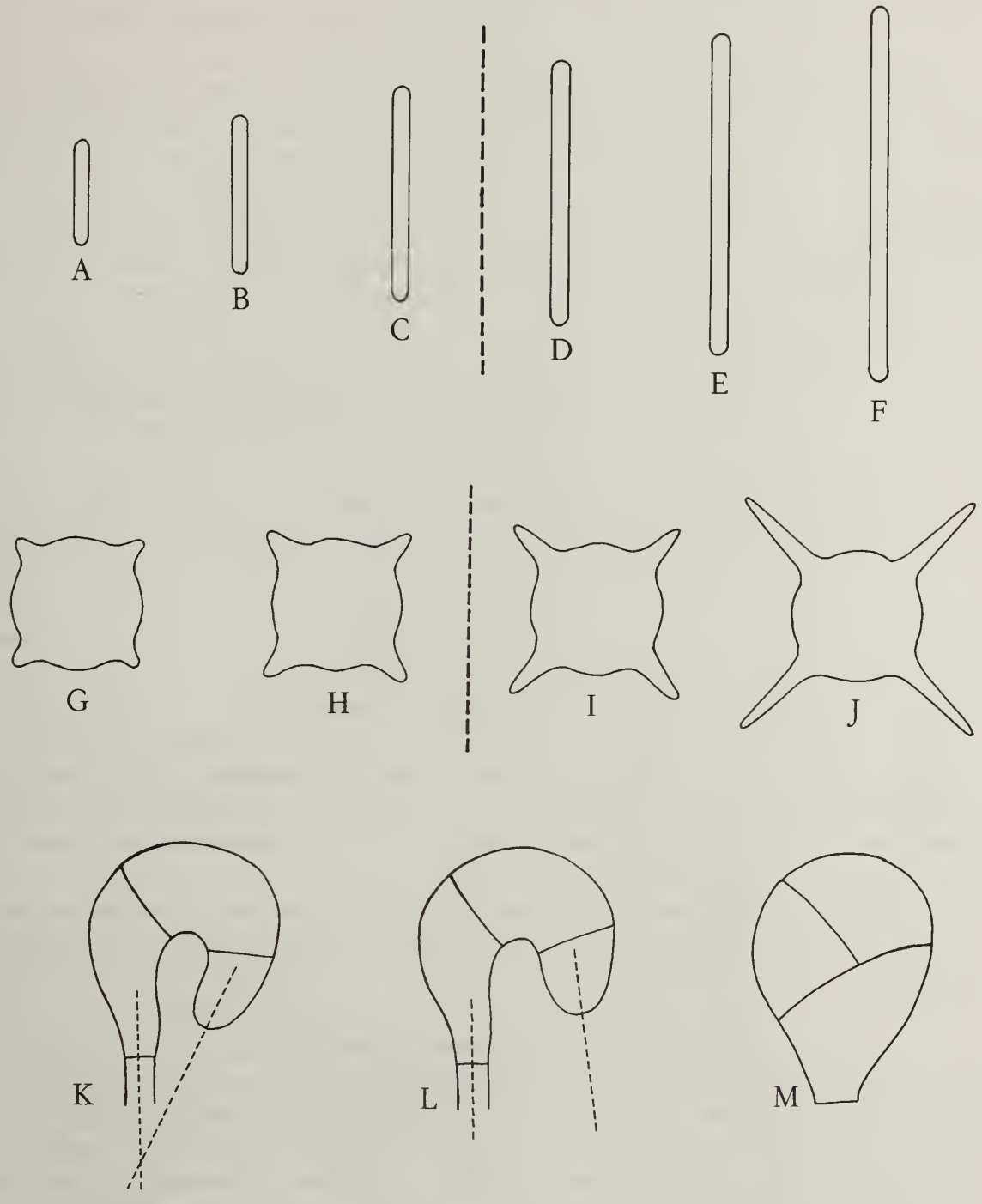

Fig. 5.2 A-C, conidia with length:width ratio less than 15:1, here considered as amerospores, D-F, conidia with l:w ratios exceeding 15:1, here considered scolecospores; G-J, conidia illustrating the minimal requirements for staurospores, G-H do not qualify because their protuberances are too short relative to the spore body, I-J qualify as staurospores because their protuberances exceed ¼ the length of the spore body; K, a 'minimal' helicospore, with axis intersecting itself; L, axis does not intersect with itself, so this conidium is not regarded as a helicospore; M, a 'minimal' dictyospore, with two intersecting septa.

we illustrate a 'minimal' dictyospore in Fig. 5.2 M.

"The scolecospore presents some problems peculiar to itself...The major difficulty lies in a definite distinction between the phragmospore and scolecospore, and the most satisfactory solution has been found to lie in the ratio between length and width...In the sphaeriales...a ratio of 20:1 represents much the most natural dividing line...[in] the Phomales ...a ratio of 10:1 is preferable." The foregoing is a passage from Clements & Shear (1931: 8-9). They had discerned one of the problems we face in this chapter. Yet it is clear that we cannot condone a 'double standard' of the sort they propose, and we have accordingly adopted what seems to us a reasonable compromise, setting the minimum length/width ratio of the scolecospore at 15:1. We had actually arrived at this figure by visual testing (see Fig. 5.1 A-F) before we read the comments of Clements & Shear.

Note that in our key we have given the more striking *shapes* priority over *septation*. We believe this is what Saccardo intended, and we also think that such shapes are often easier characters to read than is septation, particularly in narrow, colourless spores and if phase-contrast optics are not available.

Since the lines of demarcation we have drawn are very sharp, it may be asked how we would deal with fungi whose conidia ranged over two of our quantitative categories. For example, what of a collection whose conidia had length/width ratios ranging from 12:1 to 18:1? Our answer here is to measure an adequate sample of conidia, and let the *mean* decide into which category the conidia of that particular collection should be placed. This 'rule of the mean' could be used to decide all borderline cases.

Another problem inherent in this terminology is that some fungi produce conidia belonging to more than one of the categories based on septation. It is quite common for a species to produce didymospores *and* phragmospores, or phragmospores *and* dictyospores. Less commonly, a single species will form amero-, didymo-, phragmo- and dictyo-spores. Here the rule of the mean should *not* be applied, and the range in septation should be expressed either numerically, or by using the appropriate Saccardoan terms.

The terminology of spore development is beyond the scope of the present discussion, and the reader is referred to Chapters 15 and 16 in 'Taxonomy of Fungi Imperfecti' (Kendrick 1971) for a treatment of this topic.

THE 'FRUCTIFICATIONS' OF FUNGI IMPERFECTI

The word 'fruit' is variously defined, and has even more diverse connotations, but clearly began life as a general term for the kind of structure that develops from the ovary of a flowering plant after fertilization. Perhaps the most basic definition possible is 'seed(s) and accessory structures'. The accessory structures may perform such functions as protection and/or dispersal, but the constant is the content -- a seed or seeds -- almost always the result of a sexual episode.

If we transpose this word 'fruit' to the lexicon of mycology, we do it little violence in referring to structures producing meiospores -- ascospores or basidiospores -- although, realizing that the analogy is not perfect, we have tended to call these 'fruit bodies' or 'fructifications' rather than fruits. We now prefer the more specific 'ascoma' and 'basidioma'.

When we come to the Fungi Imperfecti, the use of the terms 'fructification' or 'fruit body'

seems less defensible. No sexual congress is being celebrated, no long-sought mingling and reassortment of genes being perpetuated. Just a form of vegetative reproduction. Who would call a potato, or an onion, a fruit? Perhaps we can sidestep the whole question simply by using more specific terms. Just as ascomata are subdivided into such categories as apothecia, perithecia, etc., so we have special names for different kinds of asexual 'fructification'. We commonly speak of acervuli, pycnidia, sporodochia, and synnemata or coremia.

Two major groups are currently distinguished within the Fungi Imperfecti, on the basis of differences in their sporulating structures. Hyphomycetes form their conidia on or from conidiophores that may be single or aggregated into synnemata (coremia) or sporodochia, but never develop under the shelter of any protective integument. Coelomycetes develop their conidia beneath some kind of protective integument. Most of what follows refers to the 'conidial fructifications' of the latter group, which have long been called pycnidia and acervuli, since the most contentious issues lie in that quarter.

Clearly, we must first try to establish exclusive and unequivocal definitions of these structures, since they have been given such taxonomic importance. Ainsworth & Bisby's 'Dictionary of the Fungi' (6th Edition) (1971) defines pycnidium as: "the sporocarp of the Sphaeropsidales, frequently globose or flask-like; also found in many lichens...". We must admit to being rather disappointed by this definition. It smacks of circularity. What if one looks up Sphaeropsidales and finds it defined as producing pycnidia? And what of those pycnidia which are not globose or flask-like? (Such do exist, as we shall see). What are the limits? And what kind of spores do these structures produce? Moving on to Snell & Dick (1957) we find pycnidium defined as follows: "In the Sphaeropsidales or Phyllostictales, a variously shaped cavity resembling a 'pyrenocarp' and bearing pycnidiospores which are more often called conidia." Here, at least, the function if pycnidia is mentioned, but we are not otherwise much further ahead. We would defy anyone who was not already initiated into some of the mysteries of mycology to identify a pycnidium from either of those definitions.

Unhappily, the two fragmentary and evasive definitions quoted above are symptomatic of the general lack of precision often found in discussions of Coelomycetes. It is a vagueness born of unfamiliarity on the part of most mycologists.

When it comes to defining acervulus, the Dictionary of the Fungi does better: "an aggregation of hyphae (pseudoparenchyma) which is subcuticular, subepidermal or deeper in origin and never entirely superficial, having neither specialized basal, lateral or upper wall structure nor a distinct ostiole or longitudinal line of dehiscence, and bearing conidiophores on the upper surface. cf. sporodochium." This is much more detailed, direct and precise than the corresponding definition for pycnidium. But we are still left to ascertain two important facts for ourselves: that acervuli always develop immersed in a host plant, and that they are actually elaborated as a means of producing conidia. Further, and most strange, there is no mention of the Melanconiales, the form Order which is characterized by its development of acervuli. Snell & Dick give a more comprehensive definition: "the sporiferous structure of Melanconiales, subcuticular or subepidermal and never superficial, without peridium or covering of fungous tissue and yet determinate, varying from a discoid and applanate mass of conidiophores arising from a thin hyphal weft to a thin, applanate to

thick, pulvinate pseudoparenchymatous layer or cushion, with or without setae, and usually prolifically producing conidia in a moist mass." Note that neither of the definitions we have quoted seems concerned to differentiate the acervulus from the pycnidium. Again, this can only be the result of unfamiliarity. Why are the Coelomycetes so poorly known and so inadequately defined?

The group has had a checkered history. Sutton (1973) gives an extensive account of their misadventures at the hands of mycologists. His account must be read to be believed. The best comparison we can draw is with the treatment of the North American native people by the white man -- splintered, pushed around, and all but ignored for many years, they have now begun to re-emerge as a force to be reckoned with.

Link (1809), not surprisingly, placed sporodochial Hyphomycetes, leaf and stem rusts, and acervular fungi in the same group (Order Epiphytae). Corda (1842) recognized 35 genera of Coelomycetes, but distributed them among all four 'orders' of fungi. Nevertheless some of the acervular genera were now separated from the rusts, and placed in a new family, the Melanconiaceae. And in 1845 Léveillé placed most pycnidial genera in the Sphaeropsidei. Not until 1880, however, were most of the Fungi Imperfecti disposed in the groups we use today. Saccardo characterized the Sphaeropsideae by pycnidia, the Melanconiae by acervuli, and the Hyphomyceteae by individual conidiophores, synnemata (coremia) or sporodochia. And there, for most mycologists, the situation rests, after almost a century. Does this mean that Saccardo had hit on the perfect solution? Not quite. Although Saccardo's categories have been enshrined in the pantheon of accepted mycological wisdom (i.e., used in the major compilations and identification manuals) they will not withstand careful scrutiny.

This has actually been acknowledged by a few of our more perceptive forebears. Potebnia (1910) recognizing that sporodochia are basically very similar to small acervuli without a host integument, grouped acervular and sporodochial fungi in the 'Acervulales'. Grove (1919) proposed the name Coelomycetes to cover the whole range of architecture encompassed by pycnidia and acervuli. Were these perhaps the first flickers of recognition of the biological continuum onto which we impertinently impose our taxonomic imperatives?

Some conidial fructifications are closed, or pycnidial, when young, but later open out like acervuli. Kempton (1919) called these 'pseudoacervuli'. Other conidial fructifications are intermediate in that they only partly enclose their hymenia, and these Potebnia (1910) called 'pseudopycnidia'. Von Höhnel (1923) recognized five types of conidial fructification: acervuli, stromata, true pycnidia, cupulate pycnidia and 'pycnothyria'. Sutton (1973), after a discursive prologue, chose to leave the two accepted orders, Sphaeropsidales and Melanconiales, internally undivided, since "...no system has yet been advanced that will satisfactorily accommodate or distinguish the variability and diversity in form shown by coelomycete fructifications." As long as one works on one Coelomycete at a time, it is not too difficult to apply Procrustean measures, and force each into the pycnidial or the acervular camp. Until we came to compile the Icones Generum Coelomycetum, and subsequently, with a group of graduate students, to construct a key to the genera illustrated therein, we were not moved to question the extant terms seriously. But it is now clear to us that every possible intermediate exists between the typical pycnidium and the typical acervulus, and that the

distinction between the acervulus and the sporodochium sometimes appears trivial.

Faced with a typically biological continuum, we can only suggest that a new, inclusive term is needed. We propose the term *conidioma* (plural: *conidiomata*) for all specialized, multi-hyphal, conidium-bearing structures. This term, which was suggested by Mr. John Michaelides, a graduate student in our laboratory, matches the extant terms, ascoma and basidioma. Conidioma can be a term of very wide application, embracing acervuli, pycnidia, sporodochia, synnemata and, most important, all intermediate forms. Since this term promises to be of use in the present discussion, we will adopt it immediately.

In an attempt to characterize more accurately and analytically the kinds of conidioma which have been called pycnidia and acervuli, we will adopt rather restrictive definitions of these terms.

The typical pycnidial conidioma displays three main features: (1) The conidia form more or less completely enclosed by a *fungal* integument. (2) Conidiogenous cells line more or less the *entire* cavity. (3) There is a fairly well-defined and usually restricted ostiole or mouth through which the conidia escape (It is not our purpose in this definition to differentiate between pre-formed, lysigenous and schizogenous ostioles, although we acknowledge the existence and taxonomic importance of such developmental diversity and even attempt to categorize it in Table 5.1).

Pycnidial conidiomata may be immersed in host tissue, or erumpent, or superficial. They may form in or on fungal stromata. They may be internally uni- or pluri-locular. We attempt to identify these characteristics also in Table 5.1.

The typical acervular conidioma may be defined as follows: (1) The hymenium develops beneath an integument entirely of *host* origin. (2) Conidiogenous cells are restricted to the *floor* of the cavity. (3) At maturity, there is usually a split of the host integument, and considerable exposure of the relatively flat hymenium. (4) The hymenial layer arises from a more or less well-developed *pseudoparenchymatous* stroma which forms at some level *within* the tissues of the host. This last feature is intended to distinguish the coelomycetous acervular conidioma from the sometimes very similar hyphomycetous sporodochial conidioma which, at least in our interpretation, lacks a pseudoparenchymatous basal stroma. We note, however, that in some genera, e.g., *Chaetospermum* Sacc., and *Mastigonema* Speg., these tissues may gelatinize and essentially disappear at maturity. We must also admit that we make this distinction with less than wholehearted conviction, since we actually tend to agree with Potebnia's (1910) realignment of acervular fungi with sporodochial forms.

Acervular conidiomata may develop at very specific locations within the host: these are usually described as 'subcuticular', 'intraepidermal', 'subepidermal', and 'immersed in periderm'. We recognize these categories in Table 5.1.

Our attempt to derive mutually exclusive definitions of the two time-honoured terms will help us to demonstrate just how prevalent 'typical' acervular and pycnidial conidiomata actually are among our 200 taxa. It will also show just how many almost defy such definite categorization.

Of the 200 type species of anamorph-genera described and illustrated in the ten fascicles of the Icones Generum Coelomycetum, we now consider that three, *Kabatiella*

microsticta Bub. (Icones IV:17), *Pycnofusarium rusci* Hawksw. & Punith. (Icones X:36), and *Thyrsidina carneominiata* Höhn. (Icones X:40), are actually better placed among the Hyphomycetes -- we regard their conidiomata as being sporodochial rather than acervular -- and so we have left them out of the discussion that follows. The type species of four more genera, *Diedickea* Syd. (Icones VIII:10), *Peltistromella* Höhn. (Icones X:30), *Poropeltis* Henn. (Icones VIII:32), and *Tracyella* Tassi (Icones VI:36), produce very characteristic and easily identified conidiomata which have been termed pycnothyria (Fig. 5.3 A). These are also so different from all the other conidiomata that we have excluded them from the main discussion. That leaves us with 193 taxa. Of these, we have found that 33 produce 'true acervular conidiomata' (Fig. 5.3 B) -- 10 subcuticular, 7 intraepidermal, 11 subepidermal, and 5 immersed in periderm. We do not think that many people would quarrel with our disposition of the conidiomata of these 33 fungi, although we are aware that the boundary between the acervular and the sporodochial conidioma is somewhat arbitrary, and open to revision.

At the other end of the scale, just over 100 of our 200 taxa produce what we recognize as 'true pycnidial conidiomata' (Fig. 5.3 C). The fact that they all satisfy the requirements of our three-point definition does *not* imply uniformity. As we have already mentioned, the development of the conidiomatal cavity, the ontogeny of the conidia it contains, and the manner in which the conidioma opens to release the conidia, all exhibit considerable and often elegant diversity, but a scarcity of fundamental studies cramps our style in these areas. We have stuck out our necks by listing in Table 5.1 our conclusions on the manner in which the 100 or so pycnidial conidiomata open to release their spores. Concerning the nature of the actual cavity of the conidioma, we think it probable that many will eventually be recognized as lysigenous. For the present, we must content ourselves with pointing out two genera which are described as having lysigenous cavities -- *Neopycnodothis* and *Hendersonula*. We believe there is a very strong probability that two other genera, *Kaskaskia* and *Polymorphum*, also have lysigenous conidiomatal cavities. This is clearly an area where detailed studies are long overdue. It would doubtless be most appropriate to investigate pycnidial anamorphs of the Loculoascomycetes before looking further afield.

Basically, most pycnidial conidiomata begin their development inside the host plant. Of the 103 species recognized during this study as producing 'true' pycnidia, 91 initiate their conidiomata subcuticularly, intraepidermally, subepidermally, or deeper. Many remain totally immersed in host tissue; some become partly erumpent; and a handful become almost entirely superficial at maturity. At the other end of the scale, the pycnidia of 9 species are considered 'superficial', but this is completely true in only 6 cases. In the other three species, the 'superficial' pycnidia are actually seated upon an inconspicuous erumpent stroma (e.g., *Camaropycnis libocedri*, Icones IX:9). Three further species produce their pycnidia on or in fairly massive fungal stromata (e.g., *Dothiorina tulasnei* (Sacc.) Höhn., Icones VIII:12) which are themselves erumpent, or, as reported for one species, superficial. A few species are known only from culture or in other atypical situations and so we cannot discuss the orientation of their conidiomata to a host plant.

Most pycnidial conidiomata are unilocular, but we identified those of 19 species as being sometimes or always plurilocular, and noted that 9 further species produce compound conidiomata which incorporate more than one unilocular pycnidium.

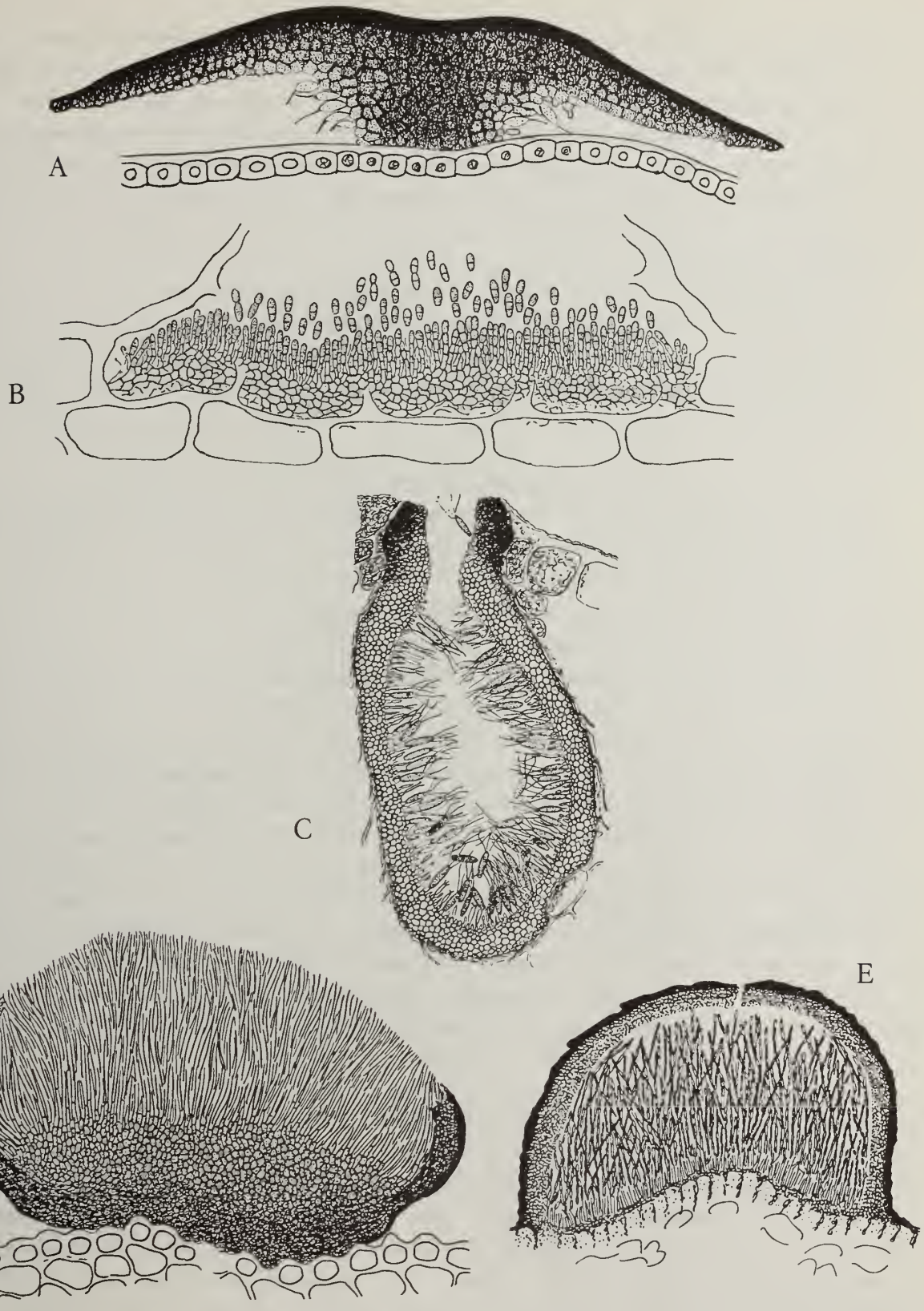

Fig. 5.3 A, pycnothyrial conidioma of *Tracyella*; B, acervular conidioma of *Staninwardia*; C, pycnidial conidioma of *Parahyalotiopsis*; D, intermediate (acervuloid) conidioma of *Pseudocenangium*; E, intermediate (pycnidioid) conidioma of *Acarosporium*.

The walls of all the 'true pycnidia' we checked are pseudoparenchymatous, though occasionally quite thin.

We tried to ascertain the manner in which the pycnidial conidiomata open to release their conidia. We consider 39 species to be originally ostiolate in the manner of a perithecium, 43 species to have a lysigenous opening in the manner of many pseudothecia, and 19 to split open in a hysterioid manner. To complete the picture we must report that two species have specialized multicellular opercula which fall away at maturity (e.g., *Neottiospora caricina* (Desm.) Höhn., Icones V:23).

From the foregoing, it will be clear that even when we define an entity like the pycnidial conidioma rather narrowly, we are not by any means eliminating heterogeneity. The purpose of this exercise is not to delineate watertight compartments of highly related organisms: that is impossible at present. We merely wish to argue for a somewhat less vague descriptive terminology than has been applied in the recent past. The more precise our terms become, and the more rigorous and searching the questions we must answer when we examine an organism, the better we will come to understand the group and its relationships, internal and external.

Between the pycnidial conidioma and the acervular conidioma as defined here lie 58 species in which the hymenium is often more or less restricted to the *floor* of the conidiomatal cavity (as in the acervular conidioma), but is at least partially roofed over by *fungal* elements (as in the pycnidial conidioma). The extent of the fungal roof varies. In most of these species it is pseudoparenchymatous, but in some it is distinctly plectenchymatous (e.g., *Colletotrichella periclymeni*, Icones III:13; *Crandallia juncicola*, Icones VII:9; *Kabatia lonicerae*, Icones IV:15), and in a few there is no more than an excipulum of setae or relatively unmodified hyphal elements (e.g., *Myxormia atroviridis*, Icones I:27). *Monochaetiella hyperrheniae* looks very acervular, but although the 'roof' is largely of host origin, the host elements are infiltrated by fungal hyphae (Icones IX:21).

In some, the opening of the conidioma is very wide (Fig. 5.3 D), giving a rather acervuloid appearance (e.g., *Coma circularis*, Icones I:13; *Diachorella onobrychidis*, Icones VIII:8; *Paradiscula spuria*, Icones IV:23; *Phaeopolynema argentinense*, Icones VI:28; *Pseudocenangium pinastri*, Icones V:29; *Seimatosporium rosae*, Icones VII:39; *Sporonema phacidioides*, Icones X:38). *Stauronema cruciferum* (Icones VI:34) is more pycnidioid than most of these, but we still regard the excipular nature of the wall as placing this fungus clearly in the intermediate group. *Mastigosporella hyalina* (Icones V:19) and *Obstipipilus malabaricus* (Icones II:27), are almost pycnidial.

In other intermediate forms, the opening is very small or absent, and the fungal roof may be many cells thick (Fig. 5.3 E). Such conidiomata, *unless sectioned carefully* to show that the hymenium is more or less restricted to the floor of the cavity, would simply be disposed as pycnidia (e.g., *Acarosporium sympodiale*, Icones VI:2; *Amerosporium polynematoides*, Icones VI:6; *Ciliochorella mangiferae*, Icones II:5; *Coniella pulchella*, Icones II:9; *Crandallia juncicola*, Icones VII:9; *Cryptosporium neesii*, Icones III:15; *Discosia artocreas*, Icones I:19; *Labridella cornu-cervae*, Icones II:21; *Leptostroma scirpinum*, Icones IV:19; *Phragmotrichum chailletii*, Icones II:33; *Polymorphum rugosum*, Icones VII:37; *Seiridium marginatum*, Icones I:35; *Sirothecium saepiarium*, Icones V:33; *Titaeosporina tremulae*, Icones III:41). A probable source of error -- or at least variation in interpretation -- is

the way in which some conidiomata change during development. For example, the conidioma of *Harknessia eucalypti* is almost closed when young, with conidiogenous cells arising from the walls as well as the base of the cavity: obviously pycnidial. But at maturity the conidioma is much more open and cupulate in appearance (Icones II:17), and could almost be described as acervular. Other species which vary in aspect between pycnidial and acervular are *Piggotia astroidea* (Icones IV:27) and *Pestalotiopsis guepini* (Icones II:31). *Angiopomopsis lophostoma* (Icones IX:3) also develops a very wide aperture and becomes cupulate.

It would appear not only safer, but also more honest, to describe these variable or discordant genera as one finds them, and instead of forcing them into the acervular or pycnidial pigeonholes, acknowledge their differences by terming them acervul*oid* conidiomata or pycnidi*oid* conidiomata, as the case may be. There seems little point in coining several new terms, or re-cycling old but obscure ones, just for the sake of naming all morphological varieties of conidioma.

CONCLUSIONS

In the interests of improving the precision of communication among mycologists, we have established what we hope are unequivocal and acceptable delimitations of the various morphologically based Saccardoan terms for fungal spores. We have also tried to analyze some aspects of conidioma morphology in what have been called the Coelomycetes. Although the 200 anamorph-species we studied may not be an entirely random or representative selection of the Coelomycete spectrum, we believe that their number is large enough for us to draw some general conclusions. Our fairly rigorous and mutually exclusive definitions of the pycnidium and the acervulus helped to clarify their status and occurrence, and resulted in the recognition of a large group of intermediate forms. We also decided that those fungi producing what we call 'true acervular conidiomata' are more closely allied to the sporodochial Hyphomycetes than to those forms producing what we call 'true pycnidial conidiomata', or to most of the intermediate group. Potebnia came to similar conclusions in 1910. In implementing such a decision, we would place some of the 'intermediates' with the acervular forms: (1) those, like *Seimatosporium roseum*, which have no fungal integument, but simply upturned or inrolled hymenial margins; (2) those with marginal setae, either separate, as in *Myxormia atroviridis*, or partly united, or completely fused into a plectenchymatous 'roof', as in *Crandallia juncicola* or *Kabatia lonicerae*. Such integuments are clearly distinct from the pseudoparenchymatous coverings found in a majority of the 'intermediate' forms, and in all the true pycnidia we examined.

Finally we note three actually or potentially productive areas of research: (1) extensive and intensive monographic and revisionary studies of 'coelomycetous' fungi; (2) studies of conidiomatal cavity or 'centrum' development in pycnidioid and pycnidial conidiomata; and (3) establishment, by observation and experiment, of connections between 'coelomycetous' anamorphs and their teleomorphs (see Chapters 12, 17).

TABLE 5.1

Analysis of Conidiomatal Morphology of 200 Coelomycetes

ACERVULAR CONIDIOMATA

subcuticular

1 *Annellolacinia dinemasporioides* Sutton
2 *Cylindrosporella carpini* (Lib.) Höhn.
3 *Monostichella robergi* (Desm.) Höhn.
4 *Myxosporina subtecta* (Rob.) Höhn.
5 *Neobarclaya primaria* (Ell. & Ev.) Kunze
6 *Oramasia hirsuta* Urries
7 *Phaeolabrella eryngicola* Speg.
8 *Septogloeum carthusianum* (Sacc.) Sacc.
9 *Septotrullula bacilligera* Höhn.
10 *Vestigium felicis* Piroz. & Shoem.

intraepidermal

11 *Crucellisporium selaginellae* Farr
12 *Discogloeum veronicae* (Lib.) Petr.
13 *Gloeosporidiella ribis* (Lib.) Petr.
14 *Melanophora crataegi* (Dearn. & Barth.) Arx
15 *Monochaetia monochaeta* (Desm.) Sacc.
16 *Stanirwardia breviscula* Sutt.
17 *Catenophora pruni* Luttrell

subepidermal

18 *Anaphysmene heraclei* (Lib.) Fr.
19 *Colletogloeum sissoo* (Syd.) Sutt.
20 *Cryptocline effusa* Petr.
21 *Fairmaniella leprosa* (Fairm.) Petr. & Syd.
22 *Gloeosporidina moravica* Petr.
23 *Leptomelanconium allescheri* (Schnabl.) Petr.
24 *Monochaetiellopsis themedae* (Kand. & Sund.) Sutt. & DiCosmo
25 *Plectronidium sinense* Nag Raj
26 *Rhabdogloeopsis balsameae* (Davis) Petr.
27 *Rhabdogloeum pseudotsugae* Syd.
28 *Scyphospora phyllostachydis* Kantsch.

immersed in periderm

29 *Asterosporium asterospermum* (Pers. ex Gray) Hughes
30 *Discula platani* (Peck) Sacc.
31 *Melanconium atrum* Lk. ex Schlecht.
32 *Phacostroma hypohermium* Petr.
33 *Stegonosporium ovatum* (Pers. ex Mérat) Hughes

PYCNIDIAL CONIDIOMATA

1 *Ajrekarella polychaetriae* Kamat & Kalani UNILOC, SIMPLE, IMMERS, SPLIT*
2 *Alpakesa yuccaefolia* (Hall) Subram. & Ramakr. UNILOC, SIMPLE, IMMERS, LYSIG
3 *Angiopomopsis lophostoma* Höhn. UNILOC, SIMPLE, IMMERS, OSTIOL
4 *Apocoryneum paspali* (Ell. & Ev.) Sutt. PLURILOC, SIMPLE, IMMERS, OSTIOL
5 *Aristastoma oeconomicum* (Ell. & Tracy) Tehon UNILOC, SIMPLE, IMMERS, OSTIOL
6 *Ascochytulina deflectans* (Karst.) Petr. UNILOC , SIMPLE, IMMERS, LYSIG
7 *Asteromella ovata* Thüm. UNILOC , SIMPLE, IMMERS, LYSIG
8 *Bartalinia robillardoides* Tassi UNILOC, SIMPLE, IMMERS, LYSIG
9 *Bellulicauda dialii* (Syd.) Sutt. UNILOC, SIMPLE, IMMERS, OSTIOL
10 *Blennoria buxi* Fries PLURILOC, SIMPLE, IMMERS, SPLIT
11 *Bleptosporium pleurochaeta* (Speg.) Sutt. UNILOC, COMPD, IMMERS, LYSIG
12 *Bothrodiscus berenice* (Berk. & Curt.) Groves PLURILOC, COMPD, STROMA, LYSIG
13 *Brycekendrickia indica* Nag Raj PLURILOC, SIMPLE, IMMERS, SPLIT
14 *Calocline chusqueae* Syd. UNILOC, SIMPLE, SUPERF, OSTIOL
15 *Camarographium stephensii* Bub. UNILOC, COMPD, IMMERS, LYSIG
16 *Camaropycnis libocedri* Cash PLURILOC, SIMPLE, SUPERF, SPLIT
17 *Camarosporellum nervisequum* (Tassi) Tassi UNILOC, SIMPLE, IMMERS, OSTIOL
18 *Camarosporium quaternatum* (Hazsl.) Schulz. UNILOC, SIMPLE, IMMERS, OSTIOL
19 *Catosphaeropsis caulivora* Tehon UNILOC, SIMPLE, IMMERS, LYSIG
20 *Ceratopycnis clematidis* Höhn. UNILOC, SIMPLE, IMMERS, OSTIOL
21 *Ceuthospora phacidioides* Grev. UNILOC, SIMPLE, IMMERS, OSTIOL
22 *Chaetoconis polygoni* (Ell. & Ev.) Clem. PLURILOC, SIMPLE, IMMERS, LYSIG
23 *Chaetodiplodia caulina* Karst. UNILOC, SIMPLE, IMMERS, LYSIG
24 *Chaetoseptoria vignae* Tehon UNILOC, SIMPLE, IMMERS, OSTIOL
25 *Chaetosticta perforata* (Ell. & Ev.) Petr. & Syd. UNILOC, SIMPLE, SUPERF, OSTIOL
26 *Chondropodiella clethrinicola* (Ell.) Höhn. UNILOC, SIMPLE, IMMERS, OSTIOL
27 *Chondropodium spina* (Berk. & Rav.) Höhn. UNILOC, SIMPLE, IMMERS, OSTIOL
28 *Ciliochora longiseta* Höhn. PLURILOC, SIMPLE, IMMERS, SPLIT
29 *Ciliosporella selenospora* Petr. PLURILOC, SIMPLE, IMMERS, SPLIT
30 *Clypeopycnis aeruginascens* Petr. UNILOC, SIMPLE, IMMERS, LYSIG
31 *Collonaemella microscopica* (Fuckel) Höhn. UNILOC, SIMPLE, IMMERS, OSTIOL
32 *Comatospora suttonii* Piroz. & Shoem. UNILOC, SIMPLE, IMMERS, OSTIOL
33 *Coniothyrium palmarum* Corda UNILOC, SIMPLE, IMMERS, LYSIG

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* Key to abbreviations: UNILOC = unilocular, PLURILOC = plurilocular, SIMPLE = simple, COMPD = compound, IMMERS = immersed, SUPERF = superficial, STROMA = stromatic, OSTIOL = with pre-formed ostiole, LYSIG = ostiole lysigenous, SPLIT = opening by hysterioid splitting, OPERC = with specialized caducous operculum.

34 *Cornutispora limaciformis* Piroz. UNILOC, SIMPLE, IMMERS, LYSIG
35 *Cyclodomus umbellulariae* Höhn. PLURILOC, SIMPLE, IMMERS, LYSIG
36 *Cytostagonospora photinicola* Bub. UNILOC, SIMPLE, IMMERS, OSTIOL
37 *Darluca filum* (Biv.) Cast. UNILOC, SIMPLE, IMMERS, OSTIOL
38 *Desmopatella salicis* Höhn. UNILOC, SIMPLE, IMMERS, LYSIG
39 *Dichomera saubinetii* (Mont.) Cooke UNILOC, COMPD, IMMERS, LYSIG
40 *Doliomyces senegalensis* (Speg.) Stey. UNILOC, SIMPLE, IMMERS, SPLIT
41 *Dothichiza sorbi* Lib. UNILOC, SIMPLE, IMMERS, OSTIOL
42 *Dothiorina tulasnei* (Sacc.) Höhn. PLURILOC, COMPD, STROMA, LYSIG
43 *Eleutheromycella mycophila* Höhn. UNILOC, SIMPLE, ? , LYSIG
44 *Eleutheromyces subulatus* (Tode ex Fr.) Fuckel UNILOC, SIMPLE, SUPERF, OSTIOL
45 *Eriospora leucostoma* Berk. & Br. UNILOC, SIMPLE, IMMERS, SPLIT
46 *Fibulocoela indica* Nag Raj PLURILOC, SIMPLE, IMMERS, SPLIT
47 *Gampsonema exile* (Tassi) Nag Raj UNILOC, SIMPLE, IMMERS, OSTIOL
48 *Gelatinosporium abietinum* Peck PLURILOC, SIMPLE, IMMERS, LYSIG
49 *Giulia tenuis* (Sacc.) Tassi ex P.A. & D.Sacc. UNILOC, SIMPLE, IMMERS, OSTIOL
50 *Haplosporella chlorostroma* Speg. UNILOC, COMPD, IMMERS, LYSIG
51 *Hendersonula australis* Speg. UNILOC, COMPD, IMMERS, LYSIG
52 *Heteropatella lacera* Fuckel UNILOC, SIMPLE, IMMERS, OPERC
53 *Hyalotiella transvalensis* Papend. PLURILOC, SIMPLE, ? , LYSIG
54 *Hyalotiopsis subramanianii* Agnihot. ex Punith. UNILOC, SIMPLE, IMMERS, LYSIG
55 *Idiocercus pirozynskii* Sutt. UNILOC, SIMPLE, IMMERS, OSTIOL
56 *Kaskaskia gleditsiae* Born & Crane PLURILOC, SIMPLE, IMMERS, SPLIT
57 *Kellermania yuccaegena* Ell. & Ev. UNILOC, SIMPLE, IMMERS, LYSIG
58 *Macrodiplodiopsis desmazierii* (Mont.) Petr. UNILOC, SIMPLE, IMMERS, LYSIG
59 *Melanconiopsis inquinans* Ell. & Ev. UNILOC, SIMPLE, IMMERS, LYSIG
60 *Microsphaeropsis olivacea* (Bon.) Höhn. UNILOC, SIMPLE, SUPERF, OSTIOL
61 *Mycohypallage congesta* (Berk. & Br.) Sutt. UNILOC, SIMPLE, IMMERS, LYSIG
62 *Mycotribulus mirabilis* Nag Raj & Kendr. UNILOC, SIMPLE, IMMERS, LYSIG
63 *Neohendersonia kicksii* (West.) Sutt. & Poll. PLURILOC, SIMPLE, IMMERS, LYSIG
64 *Neoplaconema napelli* (Maire & Sacc.) Sutt. UNILOC, SIMPLE, IMMERS, LYSIG
65 *Neottiospora caricina* (Desm.) Höhn. UNILOC, SIMPLE, IMMERS, OPERC
66 *Neottiosporina apoda* (Speg.) Subram. UNILOC, SIMPLE, IMMERS, OSTIOL
67 *Nummospora hexamera* Müll. & Shoem. UNILOC, SIMPLE, IMMERS, OSTIOL
68 *Parahyalotiopsis borassi* (Thaung) Nag Raj UNILOC, SIMPLE, IMMERS, OSTIOL
69 *Pazschkeella brasiliensis* Syd. PLURILOC, SIMPLE, IMMERS, LYSIG
70 *Pestalozziella subsessilis* Sacc. & Ell. UNILOC, SIMPLE, IMMERS, OSTIOL
71 *Pestalozzina unicolor* (Berk. & Curt.) Sacc. UNILOC, SIMPLE, IMMERS, SPLIT
72 *Phacostromella coronata* (Fuckel) Petr. PLURILOC, SIMPLE, IMMERS, SPLIT
73 *Phaeocytostroma ambiguum* (Mont.) Petr. UNILOC, SIMPLE, IMMERS, LYSIG
74 *Phaeoseptoria papayae* Speg. UNILOC, SIMPLE, IMMERS, LYSIG
75 *Phellostroma hypoxyloides* H. & P. Syd. UNILOC, COMPD, IMMERS, OSTIOL
76 *Phialophorophoma litoralis* Linder UNILOC, SIMPLE, IMMERS, LYSIG

77 *Phyllostictina murrayae* Syd. UNILOC, SIMPLE, IMMERS, OSTIOL
78 *Piringa andina* Speg. UNILOC, SIMPLE, IMMERS, SPLIT
79 *Pragmopycnis pithya* Sutt. & Funk UNILOC, SIMPLE, IMMERS, SPLIT
80 *Prosthemium betulinum* Kunze UNILOC, SIMPLE, IMMERS, LYSIG
81 *Pseudoneottiospora cunicularia* Faur. & Schott. UNILOC, SIMPLE, IMMERS, OSTIOL
82 *Pseudorobillarda phragmitis* (Cunn.) Morel. UNILOC, SIMPLE, IMMERS, OSTIOL
83 *Pullospora tetrachaeta* Faur. & Schott. UNILOC, SIMPLE, IMMERS, OSTIOL
84 *Readeriella mirabilis* H. & P. Syd. UNILOC, SIMPLE, IMMERS, LYSIG
85 *Robillarda sessilis* (Sacc.) Sacc. UNILOC, SIMPLE, IMMERS, OSTIOL
86 *Scolecosporiella typhae* (Oud.) Petr. UNILOC, SIMPLE, IMMERS, OSTIOL
87 *Seimatosporiopsis salvadorae* Sutt., Ghaff. & Abbas UNILOC, SIMPLE, IMMERS, OSTIOL
88 *Shanoria bambusacearum* (Sacc. & Syd.) Cicc. PLURILOC, SIMPLE, IMMERS, SPLIT
89 *Staurophoma panici* Höhn. UNILOC, SIMPLE, SUPERF, SPLIT
90 *Stigmella effigurata* (Schw.) Hughes UNILOC, SIMPLE, IMMERS, LYSIG
91 *Strasseria carpophila* Bres. & Sacc. PLURILOC, SIMPLE, IMMERS, LYSIG
92 *Tetranacrium gramineum* Huds. & Sutt. UNILOC, SIMPLE, IMMERS, SPLIT
93 *Tiarospora perforans* (Rob.) Höhn. UNILOC, SIMPLE, IMMERS, OSTIOL
94 *Tiarosporella paludosa* (Sacc. & Fiori) Höhn. UNILOC, SIMPLE, IMMERS, LYSIG
95 *Toxosporiopsis capitata* Sutt. & Sell. UNILOC, SIMPLE, IMMERS, LYSIG
96 *Tribolospora sycopsidis* Reid UNILOC, COMPD, STROMA, ?
97 *Trullula olivascens* (Sacc.) Sacc. UNILOC, SIMPLE, IMMERS, LYSIG
98 *Tunicago uniolae* Sutt. & Poll. UNILOC, SIMPLE, IMMERS, LYSIG
99 *Uniseta flagellifera* (Ell. & Ev.) Cicc. UNILOC, SIMPLE, IMMERS, LYSIG
100 *Urohendersonia platensis* Speg. UNILOC, SIMPLE, IMMERS, OSTIOL
101 *Vasudevella sporoboli* Chona, Munj. & Baj. UNILOC, SIMPLE, IMMERS, OSTIOL
102 *Vouauxiella verrucosa* (Vouaux) Petr. & Syd. UNILOC, SIMPLE, IMMERS, LYSIG
103 *Wojnowicia hirta* (Schroet.) Sacc. UNILOC, SIMPLE, SUPERF, OSTIOL

INTERMEDIATE CONIDIOMATA

1 *Acarosporium sympodiale* Bub. & Vl.
2 *Amerosporium polynematoides* Speg.
3 *Chaetopatella longiciliata* Hino & Katum.
4 *Chondroplea populea* Kleb.
5 *Ciliochorella mangiferae* Syd.
6 *Coleophoma crateriformis* (Dur. & Mont.) Höhn.
7 *Colletotrichella periclymeni* (Desm.) Höhn.
8 *Coma circularis* (Cke. & Mass.) Nag Raj & Kendr.
9 *Coniella pulchella* Höhn.
10 *Coryneum umbonatum* Nees ex Steud.
11 *Crandallia juncicola* Ell. & Sacc.
12 *Cryptosporium neesii* Corda
13 *Diachorella onobrychidis* (DC ex Fr.) Höhn.
14 *Dinemasporium graminum* Lév.

15 *Discosia artocreas* (Tode) Fr.
16 *Discosiella cylindrospora* Syd.
17 *Entomosporium maculatum* Lév.
18 *Furcaspora pinicola* Bonar
19 *Geastrumia polystigmatis* Bat. & Farr
20 *Hainesia rhoina* (Sacc.) Ell. & Sacc.
21 *Harknessia eucalypti* Cke.
22 *Hemidothis miconiae* Syd.
23 *Heteroceras flageoletti* Sacc.
24 *Japonia quercus* Höhn.
25 *Kabatia lonicerae* (Harkn.) Höhn.
26 *Labridella cornu-cervae* Brenckle
27 *Lecanosticta acicola* (Thüm.) Syd.
28 *Leptostroma scirpinum* Fr.
29 *Mastigosporella hyalina* (Ell. & Ev.) Höhn.
30 *Microperella quercus* Höhn.
31 *Monochaetiella hyperrheniae* Cast.
32 *Myxormia atroviridis* Berk. & Br.
33 *Neopycnodothis phyllostachydis* Kobay.
34 *Obstipipilus malabaricus* (T. & K. Ramakr.) Sutt.
35 *Paradiscula spuria* (Vest.) Petr.
36 *Pestalotia pezizoides* de Not.
37 *Pestalotiopsis guepini* (Desm.) Stey.
38 *Phaeopolynema argentinense* Speg.
39 *Phlyctaena vagabunda* Desm.
40 *Phragmotrichum chailletii* Kunze
41 *Piggotia astroidea* Berk. & Br.
42 *Plectronidium sinense* Nag Raj
43 *Polymorphum rugosum* (Fr.) Hawksw. & Punith.
44 *Polynema ornatum* (de Not.) Lév.
45 *Pseudocenangium pinastri* Karst.
46 *Satchmopsis brasiliensis* Sutt. & Hodges
47 *Seimatosporium rosae* Corda
48 *Seiridium marginatum* Nees ex Steud.
49 *Septopatella septata* (Jaap) Petr.
50 *Sirodothis populnea* (Thüm.) Sutt. & Funk
51 *Sirothecium saepiarium* Karst.
52 *Sporonema phacidioides* Desm.
53 *Stauronema cruciferum* (Ell.) Syd. & Butl.
54 *Suttoniella gaubae* (Petr.) Ahmad
55 *Titaeosporina tremulae* (Lib.) van Luyk.
56 *Truncatella truncata* (Lév.) Stey.

57 *Ypsilonia cuspidata* Lév.

UNCERTAIN

1 *Dwayalomella vaccinii* Briss., Piroz. & Pauzé - known only from culture

In the next chapter, Dr. Madelin makes a heretical suggestion: that certain modes of conidium ontogeny are not immutable, as has been widely assumed, and that their surprising plasticity may be due to relatively simple temporal or environmental factors.....

6
An Appraisal of the Taxonomic Significance of Some Different Modes of Producing Blastic Conidia

M.F. Madelin

INTRODUCTION

The last quarter century has seen the basis for classifying Deuteromycetes change from one which emphasizes the morphology of the mature conidium to one which emphasizes the processes by which conidia are generated. The new emphasis has naturally led to the critical re-examination of many anamorphs. One of the aims of so doing has been to seek features of their developmental processes which would illumine their phylogeny, and so assist in constructing a phyletic classification. The latter is more than an academic luxury. It is necessary if the classification of higher fungi is to have predictive powers of aid to industrial microbiologists, plant pathologists and others concerned with applied mycology. It is, however, open to question whether taxonomic criteria based on conidium ontogeny are *intrinsically* any more likely to lead to a classification reflecting genealogy than are the classical criteria which they have tended to displace.

Conclusions about the degree of relatedness of different holomorphs sometimes prove contradictory according to whether the evidence is drawn from the teleomorphs or the anamorphs. Such conflicts have two possible causes. Either one is dealing with:

(a) species whose *resemblances* in one state are misleadingly suggestive of *affinity;* or
(b) species whose *differences* in the other state are misleadingly suggestive of *unrelatedness.*

It is in relation to the second alternative in particular that I wish to consider the extent to which certain seemingly diverse types of conidium formation *may not necessarily* be indicative of phylogenetic diversity, and may therefore not always be obstacles to the association, in a single taxon, of holomorphs whose anamorphs have different conidium ontogenies.

PRINCIPAL MODES OF CONIDIOGENESIS

Fig. 6.1 summarizes the principal modes of conidiogenesis, details of which are described or exemplified elsewhere (Kendrick 1971, Ellis 1971). Most known anamorphs of Higher Fungi have acroauxic conidiophores with blastic conidiogenesis. Two major modes of blastic ontogeny are distinguished, according to whether all wall layers of the conidiogenous cell are involved in formation of the conidium wall or only the inner ones, and are termed holoblastic and enteroblastic respectively. Tretic ontogeny is a particular mode of enteroblastic conidiogenesis in which the conidia, clad in an extension of the inner wall of the conidiogenous cell, each emerge through a narrow channel in its outer wall. Although blastic con-

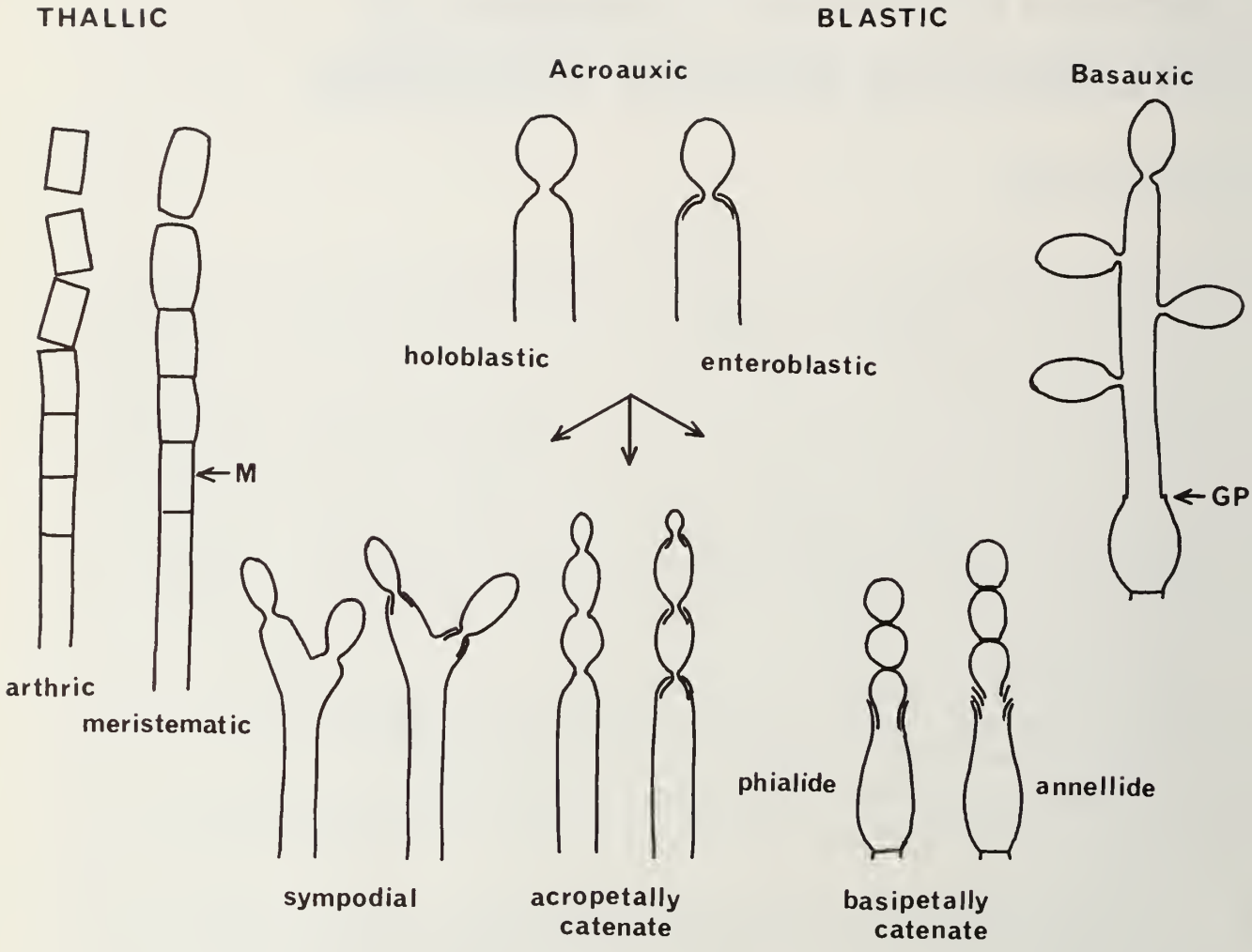


Figure 6.1. Scheme of fundamental modes of conidiogenesis. (M=meristem, GP=growth point).

idia may form singly and remain so, it is commoner for conidiophores to generate a number of conidia sequentially. There are three principal and seemingly very different ways by which this is done; namely, by sympodial proliferation of the conidiophore, by formation of acropetal chains of conidia, and by formation of basipetal chains. Whether organisms which differ in respect of such striking features as the above should be interpreted as phylogenetically distant is what will now be considered.

HOLOBLASTIC VERSUS ENTEROBLASTIC CONIDIOGENESIS

Examples of holoblastic and enteroblastic conidium ontogeny are illustrated in Fig. 6.2. One should inquire into the biological basis of this distinction. Time-lapse studies of the process of conidium development in the example of holoblastic ontogeny cited, namely *Oedocephalum glomerulosum*, show that it is relatively swift and continuous (Cook 1974). From the beginning of ampulla production to the beginning of conidium initiation takes only about 25 minutes, and there is no discernible pause in development. An hypothesis to account for the existence of holoblastic and enteroblastic modes is suggested by this swift and continuous development, namely that *the mode of blastic ontogeny is related to the juvenility or maturity of the wall at the conidiogenous locus*. If the wall is juvenile, it retains its capacity to be plasticized and have new materials intussuscepted, so that all of it can be involved in generation of the conidium initial. If, on the other hand, it has been omitted from the developmental processes for some time, it may undergo maturation changes and become no longer plasticizable, in which case new development at that locus is possible only when the mature parts of the wall are split or lysed (or both) to allow the egress of a juvenile layer from below. The postulated process of maturation might involve such chemical modifications of the wall as cross-linkage of wall polymers, melanization, or the incorporation of other materials which render wall fibrils inaccessible to the sorts of lytic and synthetic enzymes which wall growth appears to involve (Bartnicki-Garcia 1973). However, that melanin need not always be involved in the postulated change in wall properties is suggested by the fact that conidiogenesis remained enteroblastic in an albino mutant of *Alternaria brassicicola* (Campbell 1970). Besides chemical modifications, there might be the addition of secondary wall layers to generate a relatively massive structure.

The difference between the conidiogenous loci in holoblastic and enteroblastic conidiogenesis suggested in the above hypothesis is analogous to that proposed by Gay & Martin (1971) to account for the two sorts of vegetative bud production which they observed in *Saccharomyces cerevisiae*. These sorts were morphologically equivalent to holoblastic and enteroblastic development. Their differences were ascribed to differences in the age of the mother cell, which affected the properties of the wall.

The proposed explanation of the two basic modes of blastic conidium ontogeny implies that in holoblastic development the apical growth of the acroauxic conidiophore gives way to conidiogenesis with so little pause, that irreversible changes in wall structure or chemistry do not occur at the conidiogenous locus; while in enteroblastic development there is a pause sufficiently long for the wall at the conidiogenous locus to lose its capacity for direct involvement in further growth and differentiation. These implied correlations between structure and rates of development could be tested by time-lapse photomicrographic studies.

Figure 6.2. Examples of two modes of blastic conidium ontogeny at the fine-structural level. A. Holoblastic initiation of a conidium in *Oedocephalum roseum* (=*O. glomerulosum* fide Stalpers 1974). B. Enteroblastic initiation in *Alternaria brassicicola*. Drawn from transmission electron micrographs in Cook (1974) and Campbell (1968) respectively.

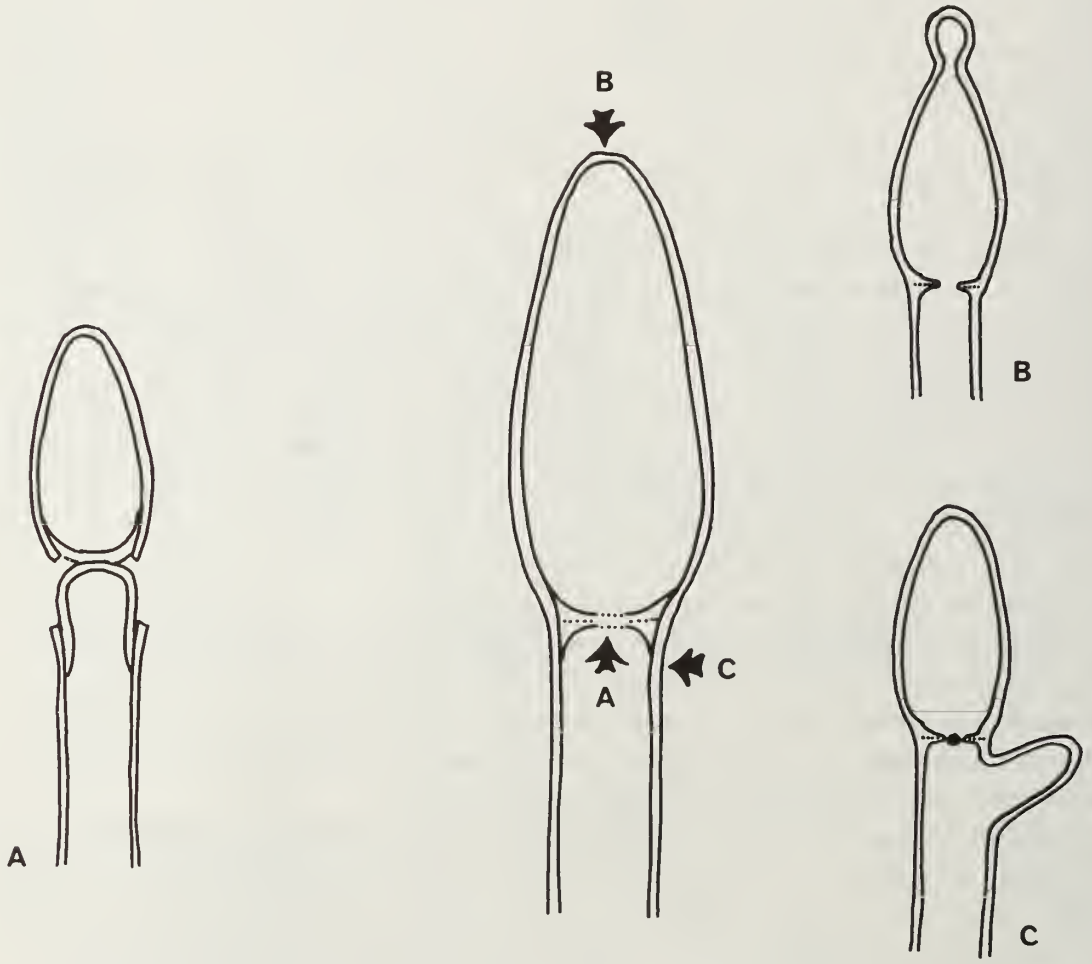


Figure 6.3. Hypothetical consequences (peripheral figures) of differences in behaviour of the septum delimiting a blastic conidium on an acroauxic conidiophore (central figure) with the potential to form a plurality of conidia. See text for explanation. A,B and C in the central figure indicate the physiologically most juvenile sites in the wall of the conidiogenous system after different sorts of septum behaviour.

At present there is a degree of support for the view the holoblastic conidiogenesis is relatively swift and continuous. Although Hughes & Bisalputra (1970) were unable to establish precise times for development in the holoblastic *Chromelosporium* state of *Peziza ostracoderma*, they did report that the ultimate branches of the conidiophores usually swelled before conidia began to develop, which implies that the conidiogenous loci consisted of physiologically juvenile wall. The latter is true also of the apparently holoblastic *Cladosporium herbarum*, in which a new conidium initial forms at the apex of the preceding one less than one hour (and sometimes even less than half an hour) after it reaches full size (Hashmi, Morgan-Jones & Kendrick 1973).

The hypothesis proposed might explain a number of unexpected fine-structural observations. Carroll & Carroll (1971) and Carroll (1972) found that the transmission electron microscope revealed holoblastic development of conidia of *Stemphylium botryosum* contrary to the expectation, based on light microscopy, that this would be enteroblastic. In order to synchronize conidiation, the material which they examined was cultured under conditions of ultra-violet radiation to induce the production of conidiophores, followed by continuous darkness to induce conidia. It is possible that pauses in development which would occur under natural conditions were thereby averted, so that when the conidiophores ceased elongating, conidium initiation followed unusually swiftly, and, because the wall at the conidiogenous locus was still juvenile, was holoblastic. The data of Carroll (1972) indicate that apical growth of the conidiophore ceased about 4 hours before emergence of the blastic conidium initial. For this species, in the sheltered conditions of a petri dish, this interval might have been too short for the apical wall to have matured so far as to compel enteroblastic development. A combined experimental and fine-structural study of *Stemphylium botryosum* would be informative. Another fine-structural study by Carroll & Carroll (1974a), on synchronously sporulating material of *Ulocladium atrum*, also failed to reveal any discontinuity between the wall of the conidium initial and the outer wall of the conidiophore, despite the expectation that conidiation in this species would be tretic (Ellis 1971). The possibility that conidium ontogeny proceeded unusually swiftly, under the special incubation conditions employed, again merits consideration. The fact that the apex of the conidiophore showed no distinct melanization at the time of conidium initiation, yet was extensively melanized only 6.5 hours later, suggests that conidia might have been produced differently if circumstances had delayed their initiation a few hours. Although Brotzman, Calvert, Brown & White (1975) interpreted their fine structural study of conidium production in *Helminthosporium maydis*, another presumably tretic species (Ellis 1971), as indicating that the process was holoblastic, it is clear from their micrographs that the major contribution to the wall of the conidium initial was from the interior tertiary and secondary wall layers at the conidiogenous locus. The dimensions of the wall layers in the conidiophore apex and the conidium initial suggest that the inner layers were capable of being distended and augmented, while the primary layer appears to have been only stretched. There is little if any evidence of its having been augmented.

Some of the problems of attempting to apply the concepts of holoblastic and enteroblastic conidiogenesis are discussed by Ellis & Griffiths (1975) in their study of *Torula herbarum* and its variety *quaternella*. The conidiogenous cells of these fungi have strongly melanized

lateral walls, but the distal wall at the site of subsequent conidiogenesis is melanized in only a thin, superficial, 'cuticular' zone. Although evagination of the distal wall to form the conidium initial was seen to rupture this cuticle, Ellis & Griffiths concluded that conidiogenesis was holoblastic, because in their view there was only a single-layered wall around the conidiogenous cell. They contended that deposition of melanin in its outer zone did not make it truly two-layered. They preferred to restrict the term 'layer' to those regions of a wall in which there was a distinct alteration in the patterns of microfibrillar orientation, or to those instances in which a new layer was laid down after maturation of the primary hyphal wall. This definition of layer is a restrictive one, and critically affects the application of the terms holoblastic and enteroblastic. There are clearly both semantic and biological problems attached to their use.

The semantic difficulties stem from the definition of enteroblastic as "a mode of blastic conidium ontogeny in which the outer layer(s) or the wall of the conidiogenous cell is (are) not involved in the conidium wall" (Kendrick 1971). 'Layers', meaning distinguishable strata, in *exterior* fungus cell walls (I deliberately exclude ascospores) can originate from: (1) interior deposition of wall material that is chemically or physically different from that on which it is apposed; (2) alteration of only part of the thickness of a hitherto homogeneous wall by chemical or physical change of materials already present, or by its impregnation with newly introduced materials or their derivatives; or (3) addition of an external pellicle, cuticle, crust or deposit by condensation of materials diffusing to the surface from within. Combinations of these processes may occur. In view of these different causes of layering, it appears that the term enteroblastic as originally defined is legitimately applicable to a number of biologically distinct situations.

Concerning the biological causes of difficulty in applying these terms, it is evident that walls in the vicinity of the conidiogenous locus sometimes differentiate layers or structures *after* initiation of the conidium (Campbell 1978, Carroll & Carroll 1974a, Ellis & Griffiths 1975), so that in order to diagnose the mode of blastic ontogeny the *earliest* stages in initiation must be examined at the fine-structural level.

Although enteroblastic conidiation is an ontogenetic phenomenon in its own right, it appears also to be an indicator of the extent of prior stratification of the wall at the conidiogenous locus. Thus it is likely that stratification into physically and chemically distinct layers can be so marked that the outer layer comes to be penetrated by the emergent interior wall layer (e.g., in *Alternaria brassicicola*; Campbell 1968), or be so mild that the outer layer stretches about the evaginating initial but is not itself augmented (e.g., in *Helminthosporium maydis*; Brotzman, Calvert, Brown & White 1975), or be so slight that the whole of the wall is evaginated and augmented in conidiogenesis (e.g., in *Oedocephalum glomerulosum*; see Fig. 3 in Cook 1974). Distinct enteroblastic and holoblastic ontogenies might thus represent extremities of a continuum which in turn reflects the occurrence of diverse degrees and rates of stratification within the fungus wall.

If blastic conidiogenesis is in fact a continuum of states, the question arises as to whether its fine characteristics can themselves serve to characterize monothetic taxa (cf. Sneath & Sokal 1973) or whether they may be expected to feature in more than one taxon. A second fundamental question is whether stratification of the wall at the conidiogenous locus,

by whatever consequence it is manifested, constitutes a good taxonomic criterion. A third is whether the mode of blastic ontogeny, as an indicator of wall stratification, serves to discriminate between degrees of wall differentiation with sufficient sensitivity to warrant its use as a prime criterion in distinguishing phyletically distinct groups.

Superimposed on the basic distinction between holoblastic and enteroblastic development are the post-initiation changes which sometimes produce complex and even localized stratification of the walls near the conidiogenous locus. At present there is probably still too little informtion to allow one to recognize whether particular features of this sort are ancient and phylogenetically significant, or merely recent and adaptive. It is, however, important to treat these developments which *follow* conidium initiation quite apart from those which *precede* it.

Because 'pores' might either exist before the conidium initial enlarges, or be created by differentiation as expansion proceeds, it appears to me desirable to preserve and emphasize the distinction between, on one hand, "porospores" as defined by Hughes (1953b), by light-microscopic critera, as solitary conidia developed *at* minute pores in the wall of the conidiophore, disregarding the question of the nature of the pore and whether or not the initial emerged *through* it; and on the other hand, "porogenous conidia" (Luttrell 1963) and "tretic conidia" (Ellis in Kendrick 1971), both of which terms imply emergence of the conidium initial *through* a pore.

THE GENERATION OF A PLURALITY OF CONIDIA ON THE ONE CONIDIOPHORE

The three principal modes of producing more than one conidium on a single acroauxic conidiophore have been listed above (see also Fig. 6.1). They appear so very different that their differences might be thought to be phylogenetically significant. However, an alternative argument may be developed.

Fig. 6.3 portrays a solitary blastic conidium initial which represents the first of what will prove to be a succession. At some time in what may be termed the 'conidiogenous cycle', that is, the cycle of events which generates a single conidium, and whose repetition generates a succession on a single conidiophore, the initial will be delimited by a septum. It is postulated that *the behaviour and properties of the delimiting septum are crucial in determining subsequent development*. The grounds for this view reside in the hypothesis, akin to that presented in the previous sections, that the longer a portion of wall is left to mature, the less likely it is to be a site for plasticizing and new growth. 'Wall' is interpreted as including septa. Conversely, the juvenility of a region of the wall of the conidiogenous cell will render it a preferred site for further generative events. With this in mind, three sorts of development in this delimiting septum may yield three consequences:

(a) If the delimiting septum forms rather late in the conidiogenous cycle and closes or becomes plugged completely, it and its lateral flanges will be the most juvenile parts of the wall of the conidiogenous system, and their consequent capacity for plastic extension and augmentation will lead to their involvement in the formation of a *basipetal* chain of conidia (Fig. 6.3 at A).

(b) If the delimiting septum, whenever it forms in the conidiogenous cycle, remains incomplete and unplugged, the apex of the first conidium will remain the physiologically

youngest part of the wall investing the conidiogenous system, and its consequent capacity for being extended and augmented (whether by holoblastic or enteroblastic processes) will lead to the formation of an *acropetal* chain of conidia (Fig. 6.3 at B).

(c) If the delimiting septum forms early in the conidiogenous cycle, but its central pore does not become closed or plugged till late, its substance may by then have become so altered by maturation processes that it is no longer the physiologically youngest portion of the envelope of the conidiogenous system. In this circumstance, a portion of the less altered original lateral wall just proximal to the septum would be the physiologically youngest portion of the conidiogenous system, and its outgrowth would generate a *sympodial* conidiophore (Fig. 6.3 at C).

Concerning the first of these three situations, numerous fine-structural studies indicate that the septa, which in phialides and annellides simultaneously delimit one conidium and constitute part of the wall of the next, form relatively late in each conidiogenous cycle, and at the time of initiation of the next conidium are still in a juvenile, relatively unmodified state. Although the distal half of the septum which becomes part of the last-formed conidium sometimes thickens or becomes electron-dense, the proximal side remains thin and electron-translucent, e.g., in *Doratomyces nanus* (Hammill 1972b), *Memnoniella echinate* (Campbell 1975), *Scopulariopsis brevicaulis* (Cole & Aldrich 1971, Hammill 1971) and *Spilocaea pomi* (Hammill 1973a). No studies of the conidiogenous cycle in basipetal systems which reveal the absolute age of the septum at the time of its involvement in initiation of the next conidium are available, but in at least a number of phialidic species the period of the whole conidiogenous cycle is so brief that the septa at that stage must in any case be young. Cole & Kendrick's (1969a) time-lapse studies indicate a conidiogenous cycle of about 2.5 hours in *Phialophora lagerbergii*, about 50 minutes in *Penicillium corylophilum*, and 20-30 minutes in the *Thielaviopsis* state of *Ceratocystis paradoxa*. In *Torulomyces lagena* it is between 2 and 3.3 hours and in *Monocillium indicum* it is from less than 35 minutes to 1.5 hours (Hashmi, Kendrick & Morgan-Jones 1972). There is less information for annellides. Cole & Kendrick's (1969b) study of *Scopulariopsis brevicaulis* indicates a conidiogenous cycle of, on average, 8 hours. In the annellides of *Subbaromyces splendens* the conidiogenous cycle is approximately 7 hours long, and swelling of a new initial apparently follows about 45 minutes after formation of a septum delimiting the preceding conidium (Cole, Hardcastle & Szaniszlo 1974). Though the conidiogenous cycle in these annellidic species is appreciably longer than in the phialidic ones cited, the critical feature is the time in this cycle at which the septum forms. The cited studies indicate that it is late, so the juvenility of the delimiting septum at the next act of conidiogenesis may be inferred.

The hypothetical situation which leads to basipetal successions of conidia invokes the closure of the septum, either by ingrowth or plugging. The primary postulate is that, by closure of the septum, the last-formed conidium is isolated from the conidiogenous system, and the possibility of its acropetal growth is precluded. Such closure could presumably be achieved adequately by plugging by Woronin bodies, should the septum itself fail to close completely. Most fine-structural studies on phialides and annellides indicate or imply complete closure of the septal pore, for example in *Coniothyrium fuckelii* (Jones 1976), *Memmoniella echinata* (Campbell 1975), *Metarrhizium anisopliae* (Hammill 1972a), *Microsphaeropsis olivaceum* (Jones 1976), *Phialocephala dimorphospora* (Carroll & Carroll 1974b), *Phialophora*

richardsiae (Olah & Reisinger 1974), *Phoma* spp. (Boerema & Bollen 1975, Jones 1976), *Stilbothamnium nudipes* (Roquebert & Abadie 1973), *Trichoderma saturnisporum* (Hammill 1974), *Ascochyta* spp. (Boerema & Bollen 1975), *Conioscypha* spp. (Shearer & Motta 1973) and *Spilocaea pomi* (Hammill 1973a). In this last species a complete new inner wall layer forms around the whole interior of the conidiogenous cell, including the proximal side of the distal septum (Corlett, Chong & Kokko 1976). Because conidium-delimiting septa develop by centripetal growth, they are always perforate when young. Hanlin (1976) believed that the narrow channel which he reported as persisting between successive phialoconidia of *Aspergillus clavatus* was so small that it was functionally not perforate. That a discernible vestige of a central pore should persist after its closure is not surprising. Pores have been seen in the delimiting septa in the annellides of *Scopulariopsis brevicaulis* (Cole & Aldrich 1971, Hammill 1971) and *S. koningii* (Hammill 1971), but Woronin bodies were nearby and were sometimes lodged in the openings, as they were in the phialides of *Ceratocystis adiposa* (Hawes & Beckett 1977a). Pores have also been seen in annellides of *Doratomyces nanus*, (Hammill 1972b) and *Pestalotiopsis neglecta* (Jones 1977), though it is uncertain for how long they remained open in relation to formation of the next conidium. By the time the next conidium initial was beginning to form on the annellide of *Trichurus spiralis*, the pore in the delimiting septum was plugged, apparently by one of the Woronin bodies which were associated with the pore from near its inception (Hammill 1977). There are two reported instances in which pores have been seen to persist till at least the next conidium initial has formed, namely *Termitaria snyderi* (Khan & Aldrich 1973) and *Thielaviopsis basicola* (Hawes & Beckett 1977b). But again, whether in living material they are occluded by Woronin bodies, as the present hypothesis would lead one to expect, is unknown. It may be significant that these species and *Ceratocystis adiposa*, referred to above, have phialides with long, close-fitting, cylindrical collarettes. The physical constraint imposed on recently formed conidium initials by the ensheathing collarette might prevent their expansion from internal pressures before their walls have consolidated, and so reduce the need for a complete delimiting septum, since the pressure differential across the septum would be less. The exceptionally vigorous and early thickening of the wall of the conidium initial of *Scopulariopsis* species might achieve the same end. The requisite degree of physiological isolation in these fungi could probably then be obtained merely by plugging.

The postulated consequence of the delimiting septum remaining incomplete and unplugged (consequence (b) above) is the development of an acropetal chain. Contrary to earlier views that open septa were a requirement if the formation of a chain was to be acropetal, the present hypothesis suggests that perforate and unplugged septa are the *cause* of chains being acropetal on potentially multi-conidial conidiophores. Fine-structural studies on acropetal chains of conidia are few, but reveal the openness of the septa until shortly before spore secession in *Gonatobotryum apiculatum* (Cole 1973), and the *Monilia* anamorph of *Sclerotinia fructigena* (Willetts & Calonge 1969).

The third sort of development, in which a delimiting septum forms early in the conidiogenous cycle but remains open till late (consequence (c) above), is exemplified by *Pleiochaeta setosa* (Harvey 1974). The basic course of ontogeny of its conidiophores and conidia is illustrated in Fig. 6.4A. The septum forms relatively early, but the continued enlargement of the initial and its growth of appendages indicate that it remains open for about three hours

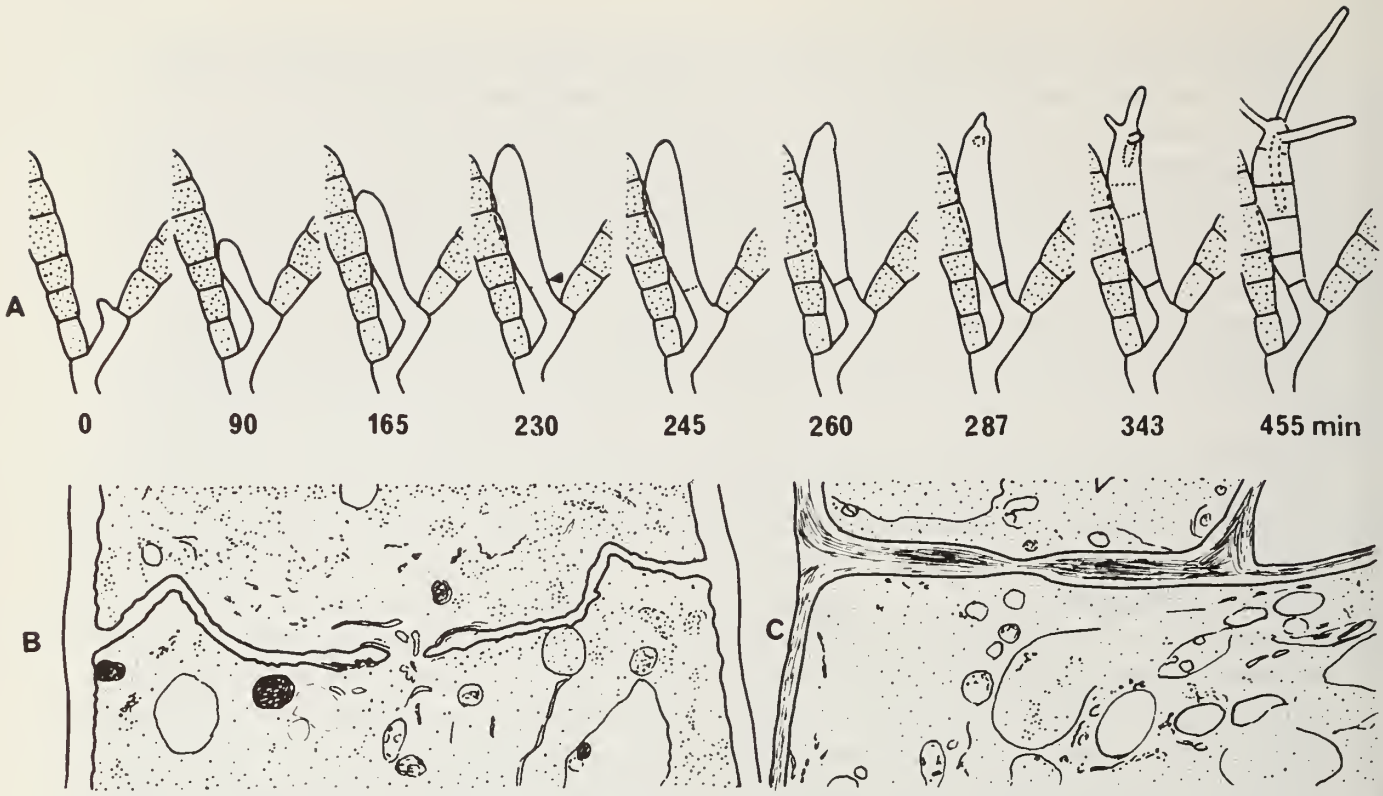


Figure 6.4. Conidiogenesis in *Pleiochaeta setosa*. A. Time-lapse sequence (time in minutes). Initiation of conidium-delimiting septum marked (▲). B. Fine-structural features of young conidium-delimiting septum. C. Fine-structural features of mature conidium-delimiting septum, immediately beneath which the conidiophore has proliferated to the right. Drawn from photographs in Harvey (1974).

Figure 6.5. Thickened conidium-delimiting septa. A. *Tritirachium roseum*. B. *Beauveria bassiana*. Drawn from electron micrographs in, respectively, Hammill (1973b) and Reisinger & Olàh (1974).

longer. Electron microscopy (Fig. 6.4B and C) confirms that this septum has undergone major changes involving thickening and the deposition of electron-dense material by the time that the initiation of the next conidium starts. According to the proposed hypothesis, by the time the septum is finally closed, thus terminating acropetal development, the septum itself is no longer a candidate site for further development, so precluding the generation of a basipetal sequence of conidia. Consequently the conidiogenous cell has only sympodial proliferation (i.e., lateral outgrowth at the next most juvenile site, which is immediately below the septum) as a means of generating several conidia on the one conidiophore.

Pleiochaeta setosa forms large conidia relatively slowly. The body of the conidium is 63-98 µm long and 13-19 µm wide (Hughes 1951). The data of Harvey (1974) indicate more than 7 hours between successive initiations. These circumstances create the opportunity for the delimiting septum to mature before the very large conidium has completed its development. It is manifestly not the case, however, that sympodial conidiophores occur only in species with large conidia. Species of some genera with sympodial conidiophores, such as *Tritirachium* and *Beauveria*, have very small ones (often 2 or 3 µm in diameter). Nevertheless, although the evidence is not extensive, it seems that these small conidia are not formed as swiftly as comparably small phialoconidia. In *Tritirachium album* successive initiations have been seen to be separated by 2 to 4 hours (Cole 1971), and in *Beauveria globulifera* by about 9 (Kendrick & Cole 1968). The opportunity for the postulated maturation changes to occur in the delimiting septa evidently exists, though we have no details of the timing of septation in the conidiogenous cycle. There is, however, indirect evidence which supports the present hypothesis. The delimiting septa in *Tritirachium roseum* (Hammill 1973b) and *Beauveria bassiana* (Reisinger & Olah 1974) are extraordinarily thickened (Fig. 6.5), especially on their proximal sides, so that it is difficult to see how they could possibly participate in formation of a new, basipetally generated initial. Thus, whatever the timing of septum development in these two species proves to be, the end result is a septum which has undergone secondary change by the time that the conidiogenous cell is ready to form the next conidium.

The evidence so far presented in support of the hypothesis that the behaviour of the delimiting septum determines the process by which subsequent conidia are formed, stems from comparative morphology. Mutations are a further source of evidence. The example of the *Cladosarum*-like mutant of *Aspergillus aureolatus* is important because it has received fine-structural study (Vujičić & Muntanjola-Cvetković 1973). The wild-type strain generates its basipetal sequence of conidia in a manner like that in other Aspergilli (Trinci, Peat & Banbury 1968, Oliver 1972, Bojović-Cvetic & Vujičić 1974, Hanlin 1976), that is, a septum forms across the base of the last-formed conidium initial and then distends to become the primary wall of the next (Fig. 6.6A). However, the mutant when grown at 26°C generates an *acropetal* sequence of blastic elements on each phialide (Fig. 6.6B). These elements remain thin-walled unless the incubation temperature is lowered to 18°C, when the terminal ones develop walls characteristic of wild-type conidia (Fig. 6.6C). Thom & Raper (1945), and Raper & Fennell (1965), theorized that the *Cladosarum*-type mutant of *Aspergillus* was a consequence of the derangement of the usual pattern of nuclear division in the phialide. The usual process generated an active and a resting nucleus, of which the latter entered the conidium initial, and the active one remained in the phialide to furnish, by way of further divisions,

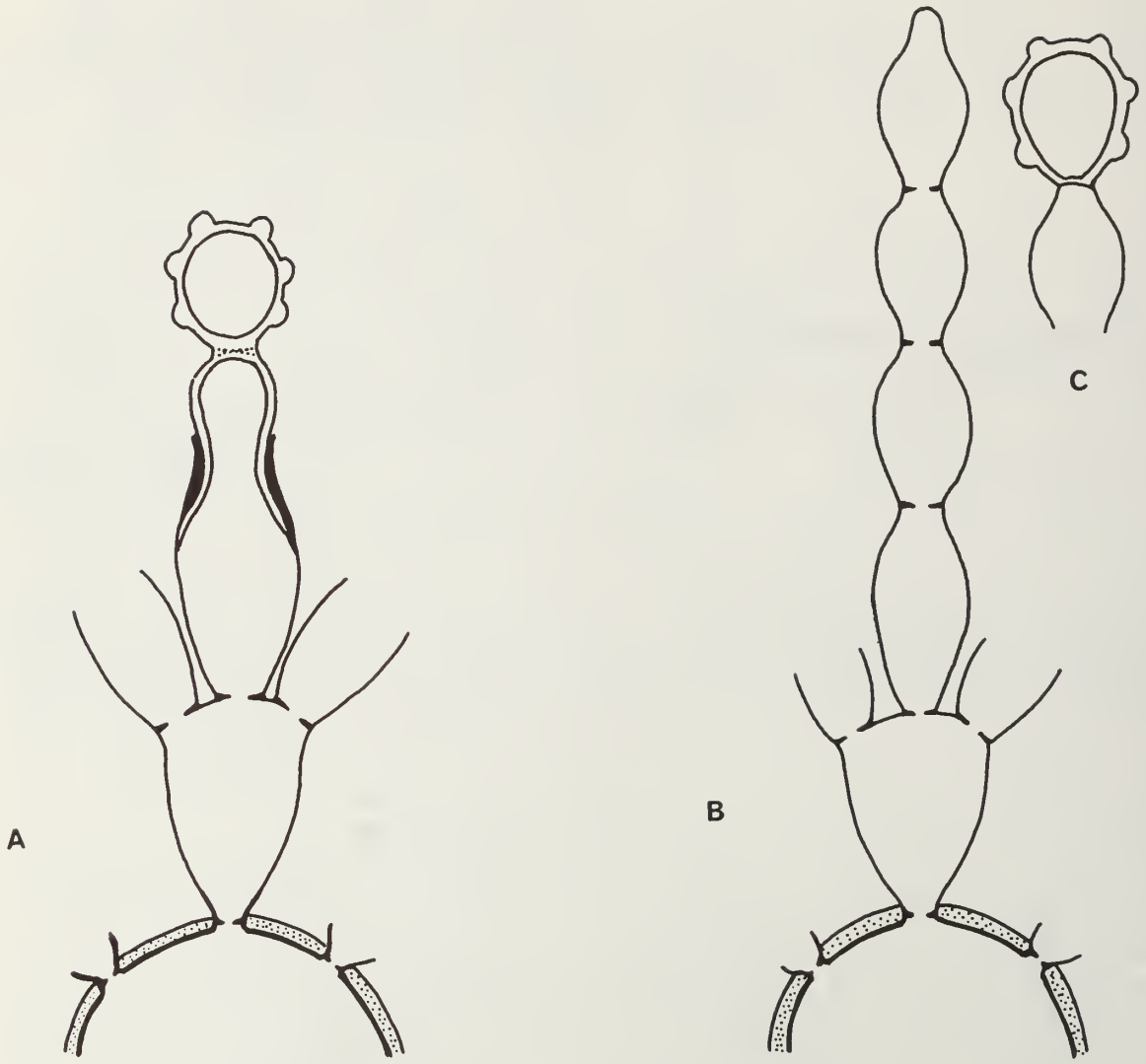


Figure 6.6. Diagrammatic portrayals of conidiogenesis in *Aspergillus aureolatus*, constructed from fine-structural data in Vujicić & Muntanjola-Cvetković (1973). A. Wild type. B. *Cladosarum*-like mutant. C. Terminal element of the acropetal chain of mutant with the characteristics of a true conidium as a result of transfer to lower incubation temperature.

resting nuclei for subsequent conidia. The hypothetical derangement led to a reversal of the normal procedure, so that the developing spore received the active nucleus and consequently proliferated to yield an acropetal chain. Zachariah & Metitiri (1971) invoked a similar polar control of nuclear activity to account for the behaviour of a structurally analogous mutant of *Penicillium claviforme*. Vujičić & Muntanjola-Cvetković (1973), however, concluded that their observations did not support Raper & Fennell's theory, because the nuclear determinism it implied failed to account for the reversion of the terminal elements of the acropetal chains to normal conidia when the incubation temperature was lowered. They concluded instead that the defect in the mutant had to be sought in its conidium wall, which could not be completely synthesized at certain incubation temperatures. Their data, however, can be interpreted in the light of the present hypothesis as indicating that the *Cladosarum* mutant arises as a result of a failure, not in general conidium-wall synthesis, but specifically in production of the septum which, in normal development, serves to delimit each conidium initiated. According to this view, it is because the septum fails to close swiftly that basipetal phialoconidium production is impossible, and acropetal proliferation replaces it.

The hypothesis presented above suggests that comparatively small changes in the behaviour of conidium-delimiting septa lead to alterations in development which compound the fundamental differences, so that three very diverse modes of conidium production ensue. The comparative smallness of the changes which are postulated as fundamental, implies that at least some of the six theoretically possible interconversions of the three modes might occur relatively readily in nature, and hence also in the course of evolution. There is some evidence that two of these interconversions do occur, at least in the laboratory.

First, change from basipetal production of conidia to acropetal formation of substituted elements has been observed in *Penicillium claviforme* (Zachariah & Metitiri 1970, 1971), and in several *Aspergillus* species: *A. niger* (Yuill & Yuill 1938), *A. fonsecaeus* (Raper & Fennell 1953), *A. nidulans* (Clutterbuck 1969) and *A. aureolatus* (Vujičić & Muntanjola-Cvetković 1973). Clutterbuck (1969) obtained 51 such mutants of *Aspergillus nidulans* generated by four different mutagens. He concluded that the activities of only a few genetic loci needed to be added to those already active in order to convert conidiophores to conidia in *Aspergillus*, even perhaps only two, of which one was responsible for the process that yielded the basipetal chains of conidia. He did not establish the primary visible site of action of this gene, but the possibility that it was the delimiting septum merits consideration.

Secondly, the possibility of interconversion of basipetal chains and sympodial proliferation is suggested by reports by Sutton & Laut (1970) (cited in Crane & Schoknecht 1973), and Fletcher (1975), that both annellides and sympodial conidium ontogeny occur in *Graphium penicillioides* and *G. putredinis*. Attempts to segregate strains with one or other mode of conidium production and to study their stability might indicate the more probable direction of evolution between these two processes.

If fungi in nature occasionally make at least some of the changes between these three modes, the taxonomic significance to be attached to their possession diminishes. Holomorphs differing in these respects need not be considered phylogeneticaly diverse. This might well be the case, for example, in the genus *Venturia*. The anamorphs of members of this genus (Sivanesan 1977, Ellis 1971, 1976) include forms with acropetal chains, basipetal chains and sympodially proliferating conidiophores (Fig. 6.7). This degree of diversity in a single

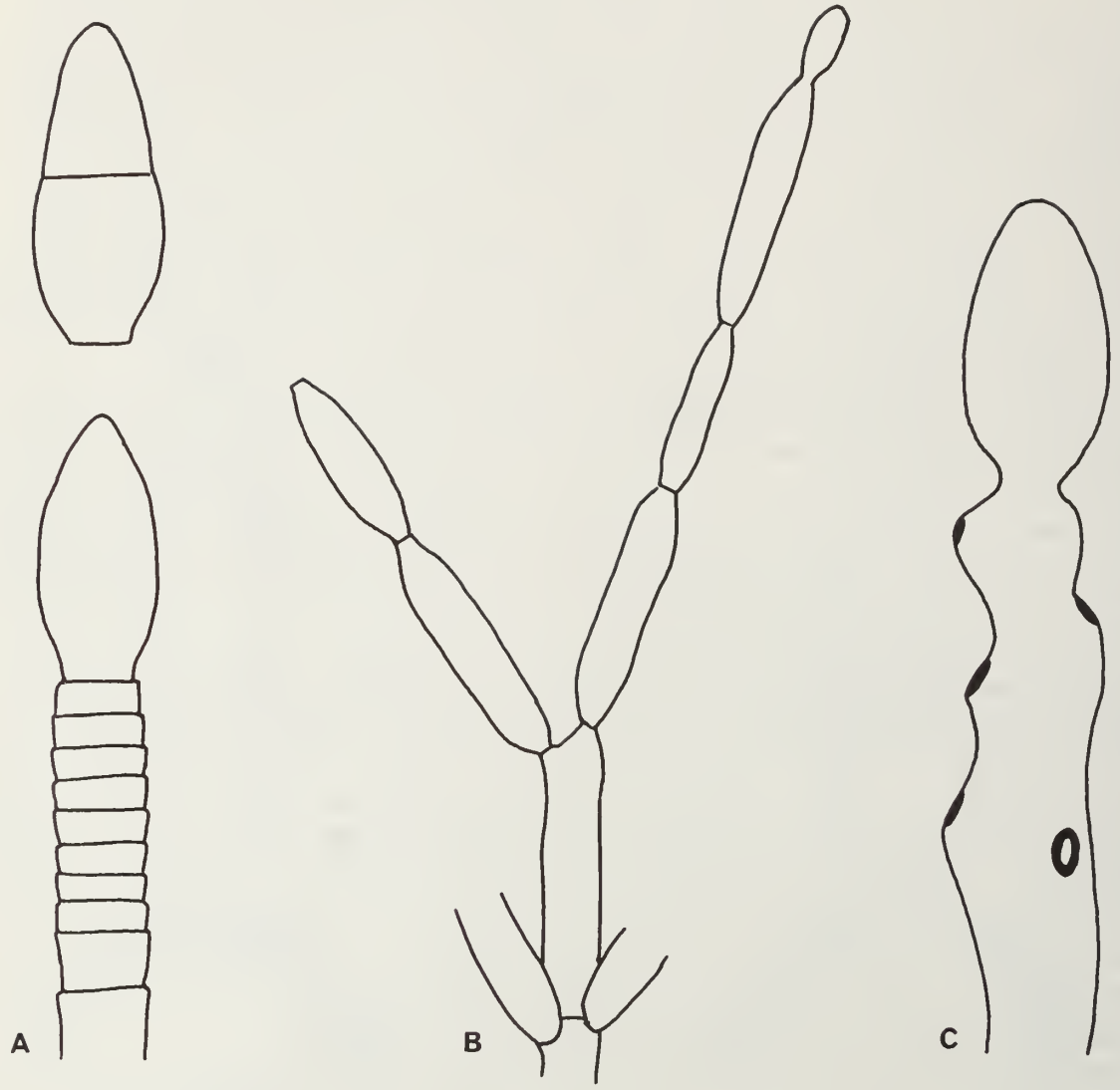


Figure 6.7. Anamorphs of *Venturia* species. A. Basipetally formed conidia of *V. inaequalis*. B. Acropetal chain of conidia in *V. carpophila*. C. Sympodial proliferation of conidiophore in *V. pirina*. (A and B redrawn after Ellis 1971. C redrawn after Hughes 1953a).

genus of genealogically related species is easily conceivable if the morphogenetic concepts suggested here prove valid.

CONCLUSIONS

The fast-growing body of data on conidium ontogeny has led to the formulation of many novel concepts such as those dealt with by the first Kananaskis Conference (Kendrick 1971). In the present essay, an attempt has been made within a limited field to take into account the rates as well as the course of some of the events in conidiogenesis, in order to interpret the relationships that exist between different modes of conidium production. With the growing recognition of the need to classify higher fungi in ways which take into account all features of the holomorph, it is becoming increasingly necessary to estimate properly the weight to be attached to the various characteristics of the anamorphs.

ACKNOWLEDGMENTS

I thank the University of Bristol and the Royal Society for grants which allowed me to participate in this symposium, and Professor Bryce Kendrick for inviting me. The essence of this paper was previously presented at an unpublished symposium of the British Mycological Society in London, England, on the 9th January, 1976.

DIALOGUE FOLLOWING DR. MADELIN'S PAPER

LUTTRELL: What you have been talking about is something that is inherent in the fungus -- the length of time it takes a septum to form and the nature of that septum; but this is also something that can be influenced by the environment. In sympodial proliferation of a conidiophore in culture, if growth is continuous, then the sympodial proliferation from below the conidium will be a blowing out of the entire conidiophore wall. If growth is slower or even intermittent (as it must often be in natural conditions, by virtue of alternating dews and dry periods, for example), then it becomes perfectly obvious, especially in forms with a brown outer wall layer, that this outer layer is simply ruptured by the sympodial proliferation. Thus the proliferation may be 'holoblastic' or 'enteroblastic' depending on external conditions -- it may simply be a matter of the age of the wall.

MADELIN: Yes: you may remember that there has been controversy over reconciling E.M. evidence of poroconidium (tretic) development with light microscope observations. It was, in fact, at Kananaskis-I that Carroll & Carroll (1971) talked about *Stemphylium botryosum*, which appeared to be holoblastic, contrary to all the expectations of light microscopists who had looked at this species. I understand that the material used by the Carrolls was produced in the laboratory using the techniques for inducing conidiation that had been worked out by Dr. Charles Leach. I suspect (and this is just a hypothesis to explain an unexpected result), that the Carrolls were simply too good at growing this fungus. Instead of letting it form its conidiophore and then have a few hours' rest before producing its conidium, they used the right sequence of light and darkness to make the whole process

almost continuous -- and I suspect that it was a rather unnatural continuity that may have resulted in the process actually being holoblastic in their material. I think electron microscopists should do some comparative studies of lab. grown and field grown material. I suspect that the pauses between conidiophore development and conidium formation inherent in the normal field development of the organism may be important in bringing about enteroblastic-tretic (or porogenous) conidium development. Taxonomic decisions have usually been based on collections of field-grown material, while E.M. studies and many other developmental studies have been based on lab. grown material, for which life may have been made too easy, so that some of the characteristics of the fungus in the wild have not manifested themselves.

KENDRICK: It is now well known that certain pathogenic dematiaceous Hyphomycetes require daylight in order to develop their conidiophore, but that this same light inhibits the formation of conidia, so that conidia normally develop only after a prolonged dark period. Presumably if these normal requirements are not respected, the fungus will react somewhat unnaturally.

We often take a dark brown wall to be a very 'set' wall and it is often in these dark brown hyphomycetes that conidia emerge through fine pores in the wall -- pores often surrounded by a thickened ring. It's almost like a germ pore -- the organism prepared the way for the next step by developing a very definite, but extremely restricted, target area for the next bridgehead.

MADELIN: I believe that *Ceratocystis* has basipetal, acropetal, and sympodial types of asexual reproduction.

KENDRICK: We documented that in our Prodromus to *Ceratocystis* (Upadhyay & Kendrick 1975).

MALLOCH: In my paper (Chap. 10) I suggest that there is a connection between the various kinds of conidium ontogeny and that this should not in some cases be weighted as heavily in systematics as it has been.

MADELIN: I'm suggesting that it needs further study. Though the end results of the various ways in which multiple conidia are formed appear so very different, it is possible that a relatively minor mutation could throw the switch at a sufficiently early stage -- and I believe that stage is located at the septum -- to lead to all sorts of differences being compounded. Looking at it from the evolutionary point of view, such switches could easily have occurred, so that related organisms might come to possess apparently very different anamorphs.

PIROZYNSKI: In *Spadicoides atra* the terminal conidium is always holoblastic, while those formed further down the conidiophore emerge through a pore. At Kananaskis I we tried to treat the development of conidia and conidiogenous cell as two separate processes. You are tending to unify them again, as being controlled, at least in some cases, by a single factor.

BENJAMIN: I was interested in the *Cladosarum* mutant of *Aspergillus:* do you regard the phialide proliferations as presumptive conidia? To use your thesis, it looks as if there has been an externally imposed delay in conidiogenesis, and the phialides proliferate until the appropriate conditions for conidiogenesis occur.

MADELIN: That was the work of Vujičić & Muntanjola-Cvetković (1973). They refer to these structures as 'pseudophialides' and also as potential conidia, but this is just semantics.

Concerning the resumption of 'normal' conidiogenesis, which you suggest would occur when conditions became suitable, I might point out that this simply doesn't happen in *Cladosarum*. The entity at the end of the chain of 'pseudophialides' does not *produce* conidia -- though it may *function* as a conidium. Zachariah & Metitiri (1971) discussed another example of this phenomenon at Kananaskis I. They had a mutant of *Penicillium claviforme* which produced acropetal chains of phialide-like conidia. They thought that this could be explained by the Thom & Raper hypothesis of a quiescent and an active nucleus. I would like to know what the septum that served to delimit the first conidium was like. My bet is that it had a persistent, open septal pore, and because of this the next conidium had to form at the top of the first conidium, and not underneath it.

From the phylogenetic standpoint, I suspect that the phialide is probably the primitive condition, because it demands astonishing precision in synchrony of nuclear behaviour and septation: the whole thing is a beautifully governed mechanism for continuous conidiogenesis. I think it likely that this structure evolved once, and other kinds of conidiogenesis have evolved from it by varying kinds of breakdowns in the precise regulatory mechanisms required by a phialide. For example, the septum delimiting the conidium in *Beauveria* and *Tritirachium* became too thick, and forced the conidiogenous cell to switch from a basipetal process to sympodial proliferation. The phialide may go back a long way -- perhaps even to the time before Ascomycetes and Basidiomycetes evolved apart.

KENDRICK: It would have to go back that far in order to explain the occurrence of phialides in rust pycnia; but Dr. Savile (Chap. 21) will have something to say about that.

CARMICHAEL: Someone asked why so many special modifications of the septum have evolved in connection with conidium production. I think it is because fungi have a problem when they release their conidia -- how to prevent rupture of both the conidium and the conidiogenous cell when they separate. So a variety of methods has been developed for plugging or preventing this potential leak -- by closing off the septal pore, or by having a very narrow connecting isthmus that can be easily plugged, or by having an empty cell between the two.

MADELIN: Our problem is in distinguishing between features that are basic to the actual process of producing a conidium, and features which represent adaptations to particular problems encountered by the organism. I am not trying to advance a *single* explanation for all kinds of septal behaviour, but I think the features I have pointed out are important and are worthy of study.

At the Second International Mycological Congress (IMC2), Tampa -- only a week or so before Kananaskis II -- a special demonstration of Fungi Imperfecti which produced more than one kind of anamorph, often at the same time and on the same mycelium, was presented by Mrs. C.J.K. Wang of SUNY, Syracuse. Once I had read Dr. Madelin's chapter, it occurred to me that it would be appropriate to ask Mrs. Wang to write up and illustrate her pleomorphic-anamorphic fungi, so that the readers of this book could be exposed to some actual examples of the phenotypic plasticity and/or diversification to be found among the Fungi Imperfecti: evidence

that may help them to throw off what Gary Samuels has called 'the curse of the single character' (Chap. 11). The single character to which I refer is that of conidium ontogeny, which has dominated the thinking of specialists for a generation.

But now Dr. Madelin has persuasively argued that some modes of conidiogenesis can be reciprocally transmuted by relatively uncomplicated environmental influences. And in the chapter which follows, Mrs. Wang shows us many examples of pleomorphism, often involving what I might call 'pleo-ontogeny', which may in some cases have begun as a result of environmental pressures, and subsequently have been genetically fixed by evolutionary pressures.

On the one hand, Dr. Madelin shows that conidium ontogeny, even in 'monomorphic' anamorphs, is by no means as stable as we might like it to be. And on the other hand, Mrs. Wang shows that a single genome can have more than one concurrent anamorphic expression, and that the sibling anamorphs can exhibit more than one mode of conidiogenesis.

Two rather different kinds of evidence, but pointing to one inescapable conclusion: we cannot hope to erect even a working classification -- let alone a 'natural' classification -- of the Fungi Imperfecti on a purely, or even principally, ontogenetic foundation.

In many cases developmental information will continue to be of great value, but it must now surely be placed in more sober perspective and viewed as just one (or one cluster) among many useful taxonomic characters. The need for new kinds of taxonomic data thus assumes a renewed urgency: and in fact the relative dearth of developments in this area is one of the reasons for our current concern with consolidating and integrating our knowledge of anamorphs and teleomorphs, the better to understand 'the whole fungus'.....

7
Pleomorphic Fungi Imperfecti

C.J.K. Wang

INTRODUCTION

Pleomorphism is much more common among Fungi Imperfecti than is generally realized. Such fungi are not restricted to particular modes of conidium formation. Many pleomorphic imperfects have a phialidic anamorph and an aleuriosporic or terminal-chlamydosporic anamorph as presented in Table 7.1 and Fig. 7.1 P. However, association of an aleuriosporic anamorph and one representing blastic conidia on sympodial conidiogenous cells is also common (Table 7.2). One state of *Calcarisporium arbuscula* Preuss (Wang D-188) has a well-developed conidiophore bearing verticils of conidiogenous cells that produce blastic-sympodial conidia at their tips (Fig. 7.2). In addition, a multicellular brown sclerotial anamorph (up to 250 μm in diam) is associated in the culture (Fig. 7.2 Sc). These sclerotia might represent abortive ascomata or pycnidia. Hughes (1951) also recorded the sclerotial anamorph in two of his isolates. A culture of *Zygosporium masonii* Hughes isolated from soil in Hawaii has conidiophores composed of several brown, billhook-shaped cells bearing two conidiogenous cells (Fig. 7.3 Z). Side by side with this typical *Zygosporium* conidiophore, a hyaline *Sporothrix* conidiophore is present (Fig. 7.3 S). This *Sporothrix* anamorph was also observed by H.J. Swart in his Australian isolates of *Z. masonii* (pers. comm.).

Some fungi have two or more different anamorphs which, though employing the same mode of conidium formation, represent different form genera. The best example is *Gliocladium roseum* (Link) Bain., in which phialidic anamorphs belonging to *Gliocladium* and *Verticillium* are present in the same culture. In many species of *Fusarium*, multi-septate macroconidia and 0-1-septate microconidia are all phialidic. The tuberculate macroconidia and the smooth microconidia of the mycelial phase of *Histoplasma capsulatum* Darling are both chlamydosporic, as are those of *Trichophyton* spp.

Increasing numbers of pleomorphic fungi are being found. Figure 7.4 illustrates a conidial fungus with both *Scopulariopsis* annellides, A, and terminal chlamydospores, Ch, produced on the same hyphae or from a single germinating conidium. A specimen with a *Selenosporella* anamorph (Fig. 7.5 Se) also produces a dark, blastoconidial anamorph (Fig. 7.5 B). In *Spadicoides canadensis* Hughes, the typical *Spadicoides* conidiophores bearing 2-celled conidia are accompanied by a dematiaceous phialidic anamorph resembling *Phialophora* (Fig. 7.6). In culture 11146, a phialidic anamorph (Fig. 7.7 P) and a dematiaceous blastoconidial anamorph (Fig. 7.7 B) are produced on the same hypha.

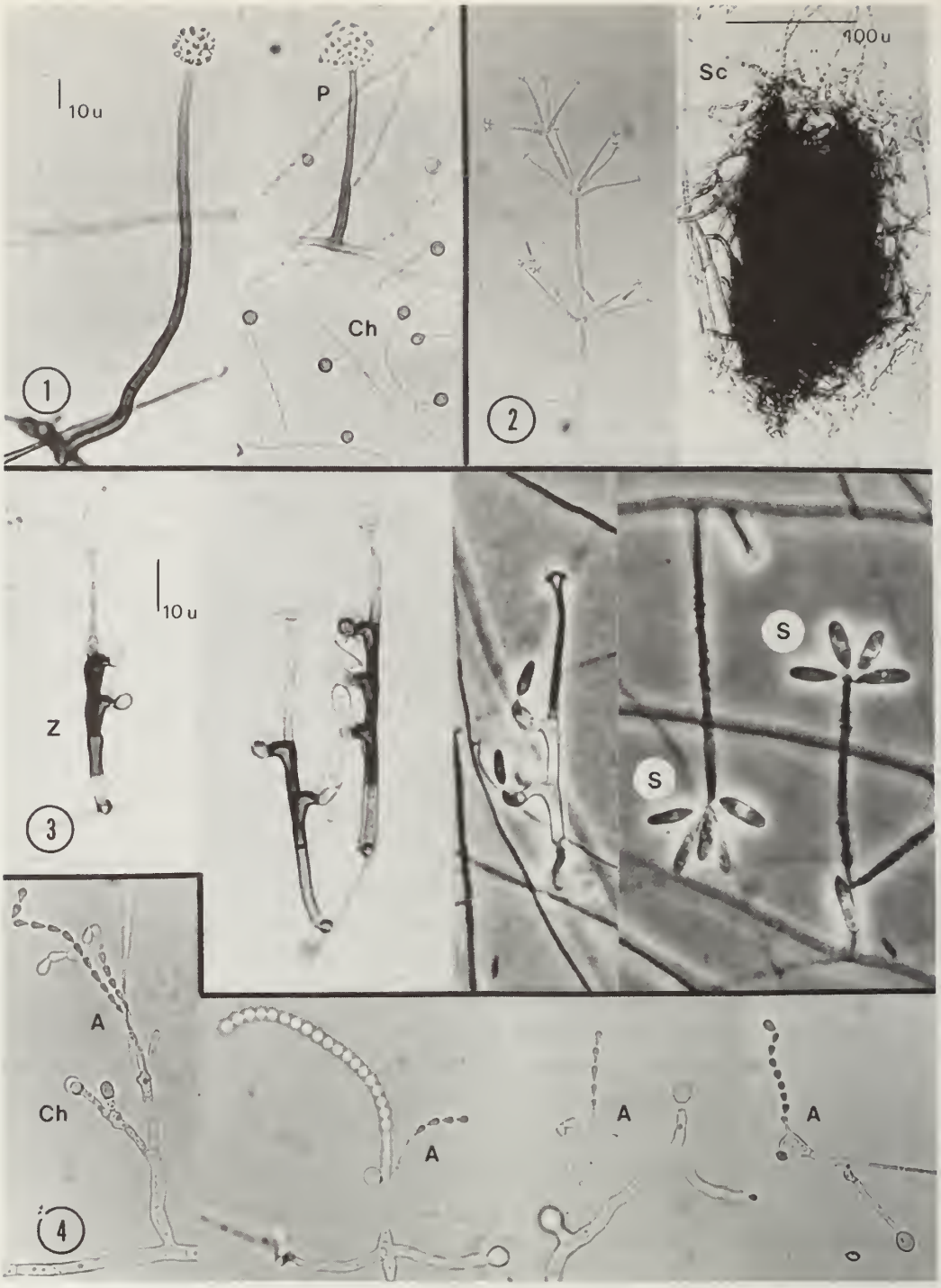


Fig. 7.1 *Chloridium chlamydosporis*, Wang 10754, phialides, P, and chlamydospores. Ch, x500. Fig. 7.2 *Calcarisporium arbuscula*, Wang D-188, conidiophore, x500, and sclerotium, Sc, x200. Fig. 7.3 *Zygosporium masonii*, Wang 1036, conidiophores, Z, and *Sporothrix* anamorph, S, x750. Fig. 7.4 *Scopulariopsis* sp., Wang C-106, annellides, A, and chlamydospores, Ch, x500.

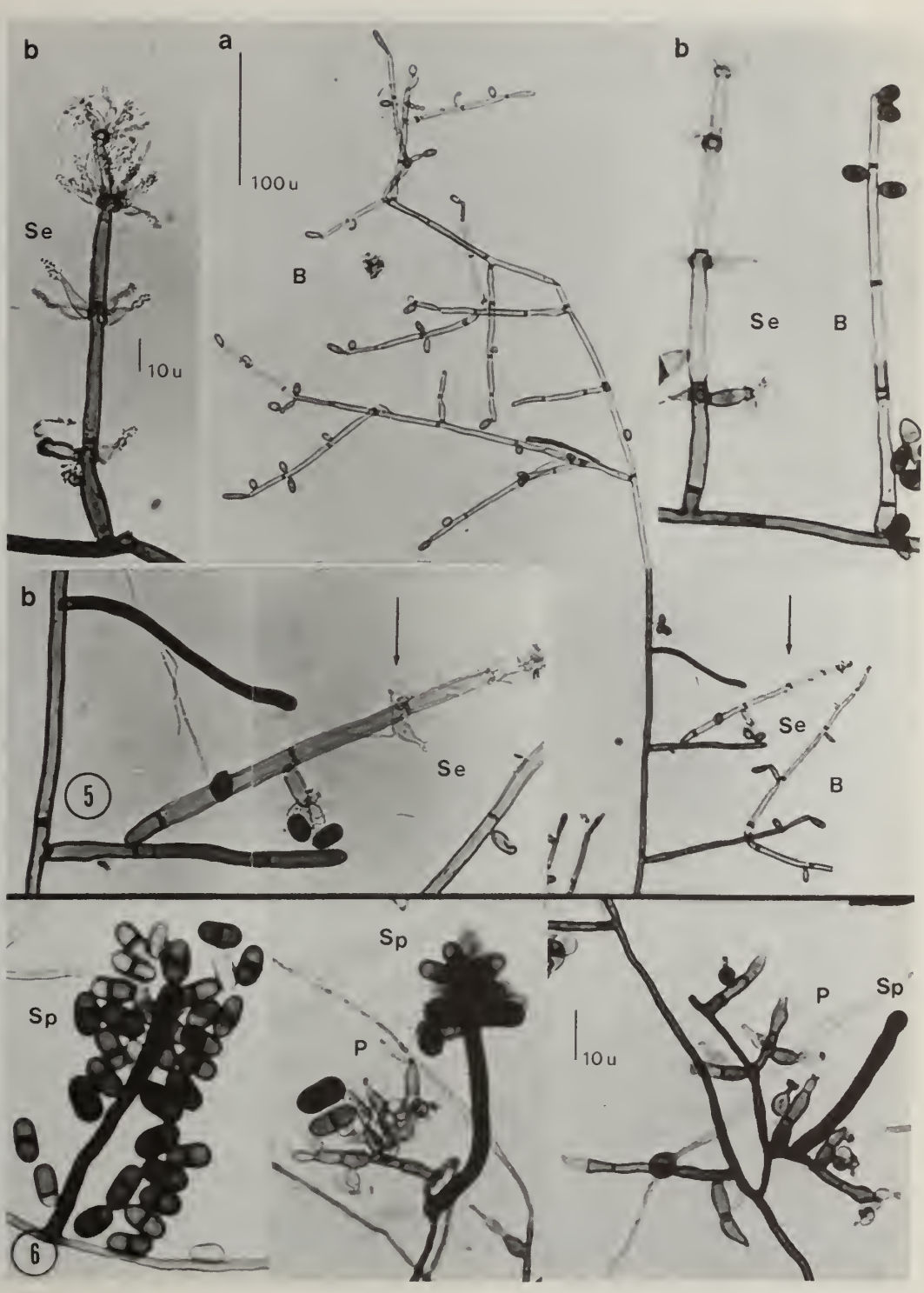


Fig. 7.5 *Selenosporella* sp., Wang 10311, conidiophores of *Selenosporella*, Se, and the dark, blastoconidial anamorph, B; a, x200; b, x500; arrows indicate the same conidiophore at two magnifications. Fig. 7.6 *Spadicoides canadensis*, Wang 11100, showing both the *Spadicoides*, Sp, and the phialidic, P, anamorphs on the same hyphae, x 750.

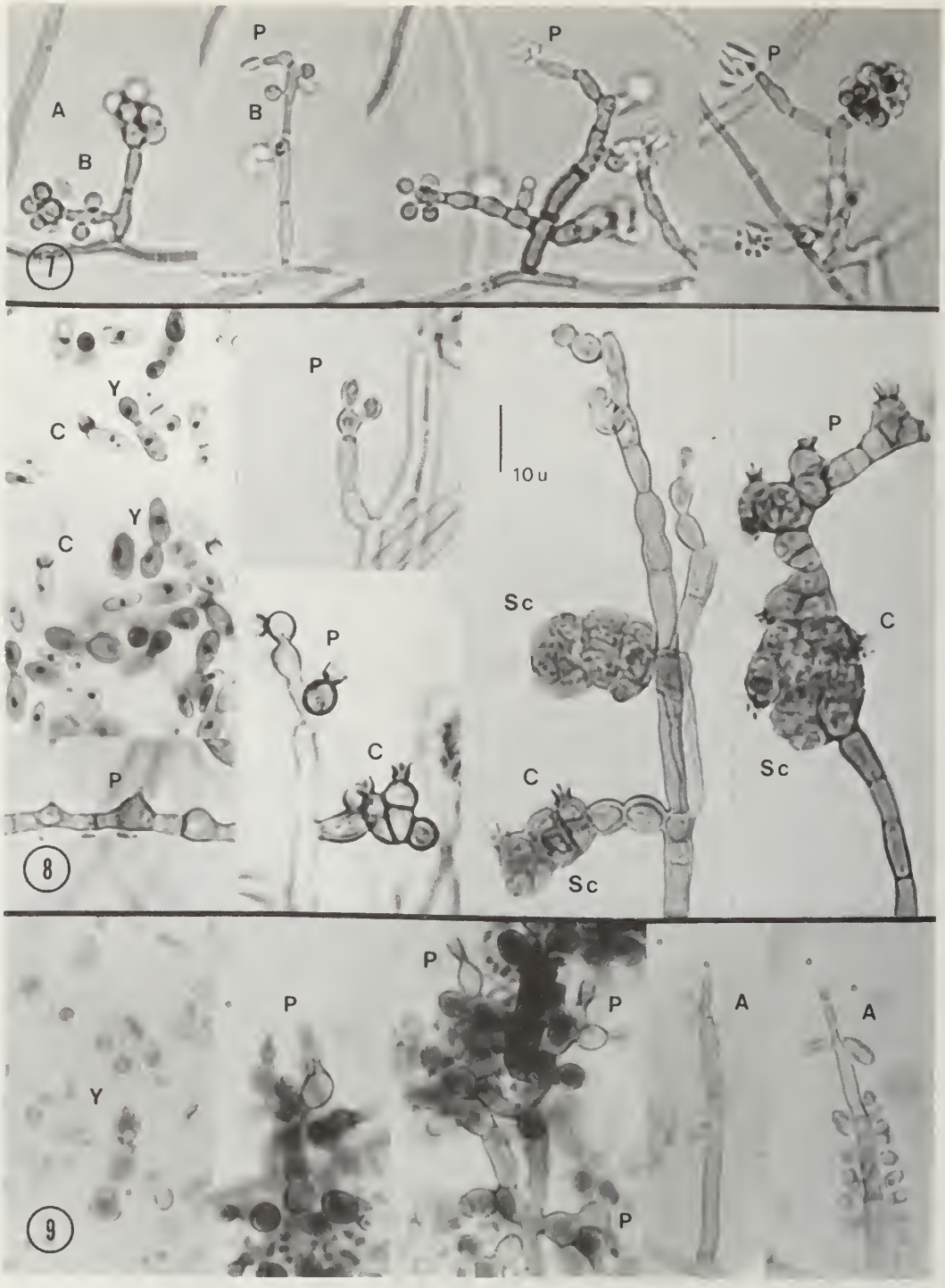


Fig. 7.7 Unidentified fungus, Wang 11146, the dark, blastoconidial, B, and the phialidic, P, anamorphs on the same hyphae. Fig. 7.8 *Phialophora heteromorpha*, DAOM 75731, yeast-like state, Y (nuclei stained with Giemsa stain), collarettes, C, phialides, P, and sclerotial bodies, Sc. Fig. 7.9 *Phialophora spinifera*, Duke 3342, type culture, yeast-like state, Y, phialides, P, annellides, A. All photos x1000.

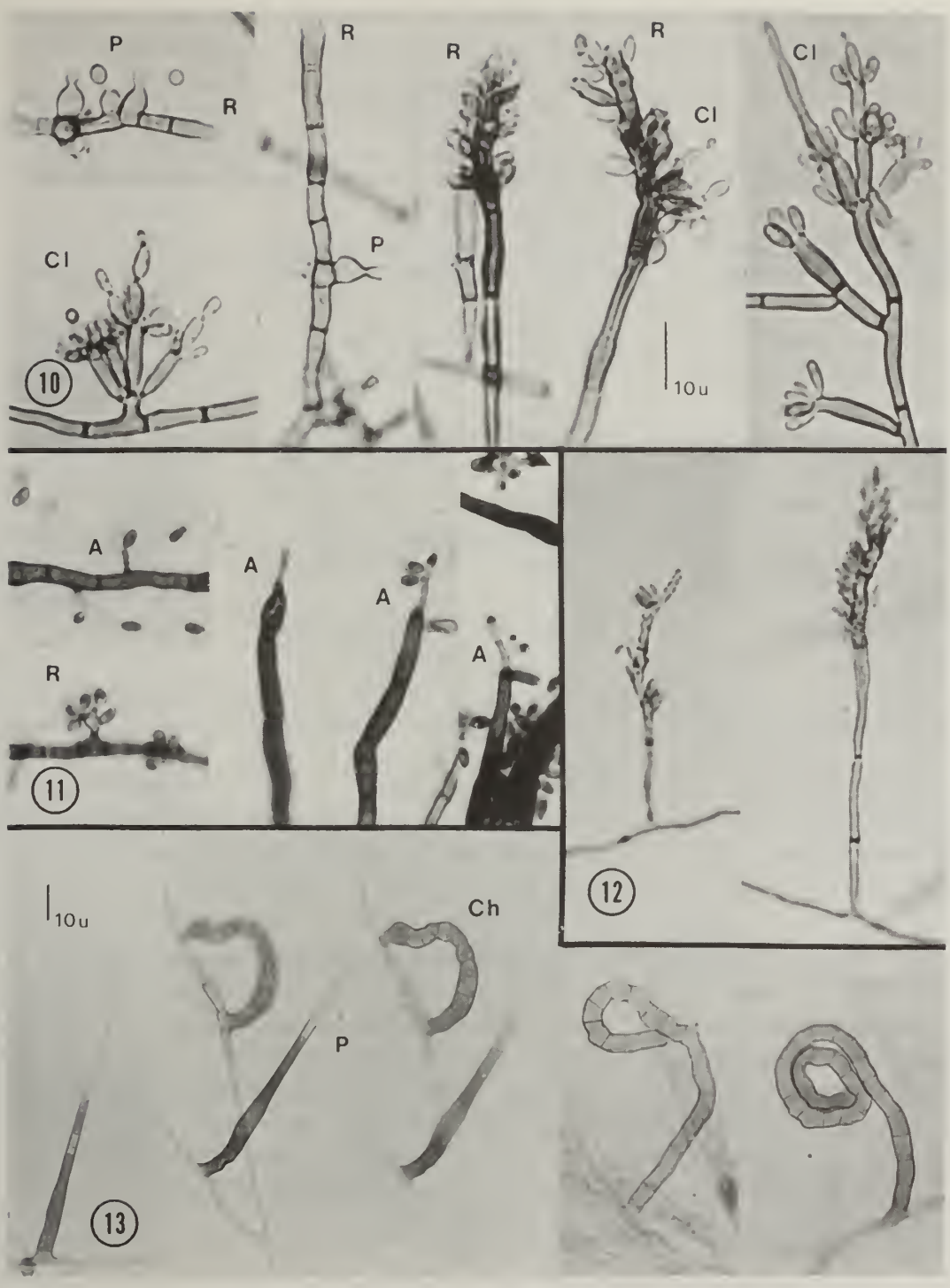


Fig. 7.10 *Fonsecaea pedrosoi*, Gordon 196-A, phialides, P, *Rhinocladiella* anamorph, R, and *Cladosporium* anamorph, Cl, x1000. Fig. 7.11 *Exophiala jeanselmei*, Wang 597, annellides, A, and one *Rhinocladiella*-like conidiophore, R (nuclei stained with Giemsa stain), x1000. Fig. 7.12 *Rhinocladiella atrovirens*, Wang 852, typical *Rhinocladiella*-type of conidiogenesis showing some denticles, x1000. Fig. 7.13 *Chalara* sp., Wang D-154, phialides, P, and chlamydospores, Ch, x500.

Table 7.1. Some pleomorphic imperfect fungi with aleuriosporic *and* phialidic anamorphs.

	Aleuriosporic or Terminal-Chlamydosporic Anamorph	Phialidic Anamorph
Acrospeira mirabilis B. & Br.	3-4-celled, apical cell rough, dark	simple; conidia catenulate
Chalara sp.	1-several-celled, dark	simple
Chlamydomyces palmarum (Cke.) Mason	2-celled, apical cell rough, dark	simple, on swollen vesicle
Chloridium chlamydosporis (van Beyma) Hughes	1-celled, smooth, dark	with collarettes
Diheterospora catenulata Kamysch.	multi-celled, smooth, hyaline	*Paecilomyces*-like
Deheterospora chlamydosporia (Goddard) Barron & Onions	multi-celled, smooth, hyaline	*Verticillium*-like
Gliocephalotrichum bulbilium J.J. Ellis & Hesseltine	multi-celled, smooth, dark	*Aspergillus*-like
Helicodendron tubulosum (Riess) Linder	helicosporous	simple, collarette
Humicola grisea Traaen	1-2-celled, smooth, dark	simple, conidia catenulate
Mammaria echinobotryoides Cesati	1-celled, smooth, dark, germ slit	simple, collarette distinct, con dia in short chain or small head
Mycogone perniciosa Magnus	2-celled, apical cell rough, dark	*Verticillium*-like
Paecilomyces varioti Bain.	1-celled, smooth, dark	*Penicillium*-like phialides with tapering tips
Sepedonium chrysospermum (Bull.) Link	1-celled, verrucose, hyaline to lightly pigmented	*Verticillium*-like
Thermomyces verrucosus Pugh et al.	1-celled, rough, dark	simple; conidia catenulate
Trichocladium asperum Harz	1-3-celled, rough, dark, germ pore	simple; conidia catenulate
Trichocladium canadense Hughes	1-4-celled, smooth, dark, germ pore	simple

Table 7.2. List of pleomorphic imperfect fungi with aleuriosporic *and* blastic-sympodial anamorphs.

Cladosporium bisporum Mats.
Cladosporium chlamydosporis Mats.
Cordana pauciseptata Preuss
Dactylaria fulva Roy & Gujarati
Dactylaria ellipsospora Grove
Dactylaria lysipaga Drechsler
Endophragmia canadensis (Ell. & Ev.) Sutt.
Idriella lunata Nelson
Raffaelea ambrosiae Arx & Henneb.
Scolecobasidium terreum Abbott
Sympodiophora stereicola Arnold
Teratosperma singulare Sydow

The literature abounds with references to pleomorphism in Fungi Imperfecti; one group that deserves special attention is the so-called black yeasts (De Hoog & Hermanides-Nijhoff 1977). Table 7.3 and Figures 7.8-7.12 show some species of this group and their morphological expressions.

Table 7.3. Morphs produced by some species of *Phialophora*, *Exophiala*, *Fonsecaea*, and *Rhinocladiella*.

	Yeastlike	Phialidic anamorph	Annellidic anamorph	*Rhinocladiella* anamorph	*Cladosporium* anamorph	Sclerotial anamorph
Phialophora heteromorpha	+	+			?	+
Phialophora spinifera	+	+	+			
Exophiala jeanselmei	+	?	+	?	?	?
Fonsecaea pedrosoi		+		+	+	
Rhinocladiella atrovirens	?	?		?		

\+ present

? rare or uncertain; reported by some authors but not confirmed by others

Phialophora heteromorpha (Nannf.) Wang has a yeast-like state in the early development of the culture; later the culture is covered with mycelium. In the yeast-like phase, cells reproduce by budding, though sometimes they form collarettes, and conidia are produced endogenously from these collarettes (Fig. 7.8 Y & C). One distinct characteristic of this species as described by Melin & Nannfeldt (1934), and later emphasized by Wang (1964), is the formation of irregular, multicellular structures that Nannfeldt termed sclerotial bodies. From these sclerotial bodies, collarettes, or phialides with collarettes, are produced (Fig. 7.8 Sc, C, P). In *Phialophora spinifera* Nielsen & Conant, yeast-like cells, annellides and phialides are all present (Fig. 7.9). *Exophiala jeanselmei* (Lang.) McGinnis & Padhye (syn.: *Torula jeanselmei* Lang., *Phialophora jeanselmei* (Lang.) Emmons, *Rhinocladiella mansonii* (Castell.) Schol-Schwarz) has an initial black, yeast-like state in freshly isolated cultures, but later the mycelial phase becomes predominant. The chief conidium producing structures are annellides (Table 7.3). Conidia produced from an annellide may not secede immediately, and thus accumulate along the sides of the tip of an annellide giving the appearance of sympodial development (Fig. 7.11). Occasionally, conidia appear to be sympodially produced on short stalks as in Fig. 7.11 R. Cultures also contain chains of moniliform cells, or toruloid hyphae, giving the appearance of *Cladosporium*-like conidiogenesis. *Fonsecaea pedrosoi* (Brumpt) Negroni, or *Rhinocladiella pedrosoi* (Brumpt) Schol-Schwarz, has typical *Phialophora*, *Rhinocladiella* and *Cladosporium* anamorphs, and these are always present in the same culture, and frequently on the same hypha (Fig. 7.10). *Rhinocladiella atrovirens* Nannf. has predominantly sympodial

conidiogenous cells (Fig. 7.12), although Schol-Schwarz (1968) claimed that it also has a phialidic state. I have seen no phialides in her culture (CBS 317.33) or in my own isolates. These genera have been studied by many investigators. The major problem confronting taxonomists is the variability of isolates. Over forty cultures of *Exophiala jeanselmei* in my laboratory can be subdivided into 3 or 4 groups. Some exhibit a more persistent yeast-like phase, others vary greatly in the size and shape of the annellide; conidial shape and measurements are also variable.

CONTROLLING MECHANISMS

Little is known concerning the mechanisms that control the pleomorphism of these fungi. This phenomenon is different from the much-studied yeast-mould dimorphism in which the alternation is subject to environmental control. Mycelial *Mucor rouxii* (Calm.) Wehmer developed globose cells and produced budding yeast-like cells under a CO_2 tension of 0.3 atm or higher (Bartnicki-Garcia & Nickerson 1962). Some human pathogenic fungi changed from a mycelial phase to a yeast-like phase when cultivated under high CO_2 tensions: 5% in *Sporothrix schenckii* Hektoen & Perkins, 10% in *Coccidioides immitis* Rixford & Gilchrist, and 15-20% in *Histoplasma capsulatum*. The mycelial *Blastomyces dermatitidis* Gilchrist & Stokes became yeast-like when incubated at 37°C (Levine & Ordal 1946). At room temperature and low CO_2 tension, the yeast-like phase reverted to a mycelial appearance.

Pleomorphism, on the other hand, has not been induced by varying one or more environmental factors. [*Editor: but see Chap. 16*] A difference in cultural media and pH slightly changed the amount of conidium production and gross morphology of the colony (Wang & Brownell 1966), but did not completely alter the microscopic characters of the fungus. Furthermore, all anamorphs of a fungus were usually found in the same culture or on the same hypha under the same environmental conditions. If the induction of a particular state is due to changes in its micro-environment, these will be difficult, if not impossible, to measure.

NUCLEAR BEHAVIOUR

Nuclear behaviour studies have not so far been particularly useful in clarifying the relationship between the number of nuclei per cell and its conidiogenesis. When nuclear behavior in *Phialophora heteromorpha, Exophiala jeanselmei* and related species was studied, Wang & Berkman (unpubl.) found that all cells, i.e., hyphae, conidiogenous cells, and conidia, are uninucleate (Figs. 7.8, 7.11). This uninucleate condition includes yeast-like cells, phialides and annellides. Because the number of nuclei per cell is not an indicator of an anamorph, it appears that pleomorphism is determined at the molecular level. It is conceivable that the regulation of those activities, whether at the level of DNA or proteins, might be influenced, to some extent, by micro-environmental conditions, though that would be difficult to demonstrate.

DEGENERATION OF ANAMORPHS

Another problem in dealing with certain pleomorphic imperfect fungi is the degeneration of one or more of the associated anamorphs in culture. Those who use cultures that have been

maintained too long in the laboratory will form a quite different concept of such fungi. A *Phialophora heteromorpha* culture (DAOM 75731) initially had abundant phialides and sclerotial bodies; after 18 years in my laboratory, the culture is now sporulating poorly. In older cultures of *Phialophora spinifera* the phialidic anamorph is scarce or absent. In most of my *Exophiala jeanselmei* cultures, the yeast-like phase is no longer present. This leads to fundamental questions concerning the taxonomy and nomenclature of such imperfect fungi.

NOMENCLATURE

After discussing the Anatomical, the Botanical and the Botanico-anatomical systems of nomenclature of the imperfect fungi, Hennebert (1971) proposed the use of his Botanico-anatomical system and provided the following interpretation:

> "The binomial of the imperfect species is thus composed of a botanical epithet, which covers the whole species and must be the oldest legitimate one, and of a form-generic name based on one of the states of the species. The form-generic name for a species will be, within the state, the oldest legitimate name. Between possible correct form-generic names for different states of the species, the choice will depend upon the judgment of the taxonomist.
>
> The form genera are allowed to contain all kinds of imperfect species, monomorphic and pleomorphic, but they remain of monomorphic value by the typification of their names. The system does not prohibit the creation of genera for the accommodation of pleomorphic fungi, but it requires the designation by the original (or a later) author of the typical state (holostatus or lectostatus) of the type species. Thus *Chalaropsis* Peyronel, based on chlamydospores and phialidic conidia, requires designation of the lectostate of its type species (the chlamydosporic state) before a monomorphic concept of the generic name can be established (Hennebert 1968)."

Hennebert discussed several advantages of the Botanico-anatomical system of nomenclature. However, the choice of generic name for a pleomorphic fungus continues to be an arbitrary one. Contrary to Hennebert's treatment of *Chalaropsis*, Nag Raj & Kendrick (1975), in their monograph on *Chalara* and related genera, reduced *Chalaropsis* and *Thielaviopsis* to synonymy with *Chalara* which is characterized by the phialidic state. They emended the genus *Chalara* to include fungi with chlamydospore states. My culture D-154, isolated from litter in an oak forest, shows a typical *Chalara* state and a curved, multicellular, dark brown chlamydospore state (Fig. 7.13) that does not belong to either *Chalaropsis* or *Thielaviopsis*. Hennebert's treatment of this fungus would have been the creation of a new genus based on the chlamydospore state. To avoid the proliferation of monotypic genera and later synonyms, it seems best to deposit this fungus in the genus *Chalara* and describe it as a new species.

The Botanico-anatomical system of nomenclature does not consider the problems of instability or degeneration of one or more states in a pleomorphic fungus. The Hawaiian isolate of *Zygosporium masonii*, after 10 years in culture, is now reduced to only the *Sporothrix* anamorph. Should this culture be re-labelled *Sporothrix*? I think not. Others may not agree. Because the type culture of *Phialophora spinifera* has degenerated and lacks the distinct phialidic

anamorph as shown in Fig. 7.9, McGinnis (1977) made the new combination *Exophiala spinifera*, whereas De Hoog (1977) transferred this species to the genus *Rhinocladiella*.

Examination of type cultures is an important and necessary procedure in the study of the imperfect fungi. However, in view of the instability of conidium production of cultures, additional rules should be established for the description of new taxa. Besides the description of the culture, photomicrographs and/or drawings should be provided; dried cultures containing all anamorphs should be deposited with the type culture; permanent or semi-permanent slides should also accompany the culture. These more stable articles will allow later workers to compare accurately their isolates with the type and the original description.

In conclusion, the need is increasing for a new nomenclatural rule in dealing with pleomorphic imperfect fungi. It is too early to propose any definitive solution to this complex problem of nomenclature. More study must be done to reveal the incidence of pleomorphic imperfects, the relationships among various anamorphs, the variability of anamorphs, and the mechanisms controlling their morphology. With better information at hand, we may hope that a reasonable nomenclatural system can be devised.

At present, more attention should be given to the study of the mechanisms of pleomorphism. Investigations that combine cytochemistry and electron microscopy may shed some light on the regulatory processes. A thorough understanding of pleomorphic imperfect fungi will improve the classification of Deuteromycetes and perhaps clarify speculation on the phylogeny or evolutionary sequence of these fungi.

ACKNOWLEDGMENTS

I wish to express my appreciation to Drs. J.L. Lowe and D.H. Griffin for reading the manuscript and for their valuable suggestions. I am grateful to Ms. Roberta Berkman for her work on the nuclear behavior of several fungi, to Drs. S.J. Hughes, M.A. Gordon, H.S. Nielsen, Jr., and Centraalbureau voor Schimmelcultures for providing cultures, and to Dr. Clark Rogerson, Editor of the New York Botanical Garden Memoirs for permission to reproduce Fig. 7.6.

As a postscript to Mrs. Wang's paper, I would like to mention some gleanings from Matsushima's beautifully illustrated book 'Icones Microfungorum a Matsushima Lectorum' (1975). He illustrates several Hyphomycetes as processing additional anamorphs which have not previously been reported. Endophragmia canadensis *(Ell. & Ev.) Sutton is shown with a conspicuous and characteristic* Selenosporella *state (Pl. 135). Similar states are also illustrated for* Acrodictys bambusicola *M.B. Ellis, (Pl. 149) and for* Teratosperma singulare *Sydow (Pl. 349).* Dactylaria dimorpha *Mats. is shown as possessing a* 'Verticicladiella' *state (Pl. 182), although it might not have been unreasonable to ascribe this state, too, to* Selenosporella.

Matsushima also attributes what he called an Aspergillus *state to* Sympodiella laxa *Subram. & Vitt. (Pl. 249), although the photomicrographs do not suggest* Aspergillus *or any other described genus to me.*

These observations are very interesting in that most of them report additional anamorphs

not mentioned in the original descriptions of the taxa involved. In particular, the occurrence of Selenosporella *in association with such disparate hyphomycetous genera as* Endophragmia, Acrodictys, Teratosperma *(and possibly* Dactylaria*), as well as the unnamed dark blastoconidial anamorph already discussed by Mrs. Wang, raises the suspicion that it may be a hyperparasite, rather than an extra phenotype. We must always be on guard for such possibilities.*

The book now broadens and deepens its horizons to consider fungal biogeography and evolution on a global scale. The next chapter concludes with a discussion of the possible ways in which anamorphs evolved, and sets the scene for the detailed treatments of specific groups of Ascomycetes and anamorphs that follow.....

8
A Biogeographic View of the History of Ascomycetes and the Development of Their Pleomorphism

K.A. Pirozynski & L.K. Weresub

INTRODUCTION

The pleomorphism exhibited by members of the Eumycota, especially rusts and Ascomycetes, may be as old as those fungi themselves. Speculating on the phylogeny of rust fungi, Savile (1976) has convincingly elucidated the direction of their evolution, which led him to conclude that pleomorphism in this group of fungi was elaborated in the dawn of their history in the Palaeozoic. Savile built his deduction on host-parasite relationships and the well-founded postulation that the antiquity of the host reflects that of its parasite and vice versa. As Savile demonstrated, the rust fungi lend themselves well to this approach: they are obligately parasitic and strongly host-specialized, and the life histories of many individuals -- despite the morphological and trophic divergence of their anamorphs -- have been fully elucidated.

The situation in Ascomycetes is different. Here the patterns of host-parasite relationship in space and time are obscured by the sheer numbers of species and the multiplicity of their morphological, physiological and ecological diversifications. Our knowledge of the life histories and geographical distribution of individual Ascomycetes is still fragmentary. Our system of classification is inadequately unified and therefore of little predictive value. And all these problems stem, in large part, from our traditional failure to cope with the pleomorphism of these fungi.

Taxonomic criteria derived from the organization and ontogeny of the centrum, which have led to a more nearly phyletic classification than the frankly artificial one of Saccardo, have not wholly withstood the test of more recent studies. The significance of the distinctive features of centrum-differentiation in the bitunicates has encountered doubt (von Arx & Müller 1975). And now the very foundation of this relatively new system -- the division into two basic ascus-types -- is being questioned (von Arx Chap. 13), because the boundary between the two lines breaks down, not in what we take to be primitive relic groups, but in groups that appear to be in their evolutionary prime.

Even the position of an ancestral *Taphrina* at the base of the dikaryomycotan dichotomy is in some peril. It will be remembered that the association of the Taphrinales with pteridophyte and mainly woody dicotyledonous hosts in a pattern strikingly similar to that of primitive rusts, coupled with *Taphrina*'s simple life history and lack of morphological specialization, indicated to Savile (1955, 1968) its place among the oldest surviving Ascomycetes. Savile considers *Taphrina* to be a conservative direct descendant of a fungus ancestral to the

Dikaryomycota, although his own phylogenetic principles stress that today's representatives of primitive fungi are unlikely to have retained the original simplicity of the reproductive mechanisms of parental groups. The very characteristics used by Savile to establish the primitiveness of *Taphrina* take on a different aspect when viewed from a different angle. In the dimorphism exhibited by *Taphrina*, wherein discharged meiospores of the parasitic sexual phase initiate a saprobic yeast phase, the yeast cells resemble ascomycetous yeasts in gross morphology, but the colonies are reddish (Roberts 1946, von Arx et al. 1977), a characteristic more usually basidiomycetous. The long-known characteristics of a dominant dikaryon phase in the life cycle, the orientation of the spindle in the first division of meiosis (Lohwag 1934), the occasionally exogenous meiospores, and the presence of an ascus-bearing cell comparable to (perhaps homologous with) the probasidium of some Heterobasidiomycetes: to some mycologists these characters conjure up a picture of a Basidiomycete -- not primitive, but highly evolved and simplified, a dead-end offshoot. Nevertheless, such a view is possible only to those who can ignore the fact the *Taphrina* produces a key organ which, by definition, is much more an ascus than a basidium. Furthermore, as Savile reminds us (pers. comm.), ancient obligate hosts (ferns, woody and early Laurasian dicotyledons for *Taphrina, Osmunda* -- even older than the Polypodiaceae -- for *Mixia*) are unusual fare for "dead-end offshoots"; meiotic spindle orientation seems to depend largely on spatial proportions in the containing cell; and the simple septum of *Taphrina* looks too much like that of Ascomycetes and rusts to be viewed as descended from the dolipore septum of Basidiomycetes. In any case, whatever the future disposition of *Taphrina* may be, further studies (on its biochemistry, wall composition, etc.) must be made before a solution to this enigma can be found. For our present purpose, *Taphrina* will be set aside, as we proceed to take a biogeographic look at less controversial groups of Ascomycota, in the hope of gaining some insight into the history and evolution of these fungi.

BIOGEOGRAPHY

Lower vascular plants, although attacked by fungi, are either relatively free of ascomycetous parasites (e.g., *Ginkgo*, Cycadaceae), or support a heterogeneous assemblage of odd members of predominantly angiosperm-associated taxa that appear to have rather recently adapted themselves to these more ancient plants (e.g., *Selaginella, Equisetum*), usually in ecological niches shared with their primary hosts. A case in point is the Phacidiales, whose members have 'jumped' to *Lycopodium* and ferns only in the area of the parasites' greatest abundance and diversification, in the boreal forest ecosystem, on Pinaceae and woody ectomycorrhizal dicotyledons. The more ancient the hosts, the more obvious is the scarcity of specialized groups of primary ascomycetous parasites. This rarity can, perhaps, be more easily explained by the absence of Ascomycota during the era of rapid evolution and dominance of their potential hosts in the Palaeozoic and the early Mesozoic, than by a subsequent unilateral extinction of the parasites. But the general paucity of Ascomycetes on ancient hosts underscores the occurrence of a small group of the Parmulariaceae on ferns and austral gymnosperms, a specific association of certain Coryneliaceae with podocarps, and of many Phacidiales with northern conifers. The distribution of these groups of Ascomycetes deserves more detailed examination.

The Parmulariaceae

The Parmulariaceae are sometimes cited as examples of fern parasites. Ferns, however, constitute only a small sector of their host range. In the family as circumscribed by both von Arx & Müller (Müller & von Arx 1962, von Arx & Müller 1975) and Luttrell (1973), of the twenty genera common to their treatments, species of only five genera occur on ferns, and only two of these genera are confined to ferns. Others parasitize conifers and angiosperms belonging to seven families of monocotyledons and thirty-eight of dicotyledons.

Even at a cursory glance, the Parmulariaceae can be seen to be pantropical in distribution, and show a strong preference for evergreen host plants. However, a close look at their geographic distribution and host range reveals more complex and interesting patterns (Map 8.1). The centre of their greatest diversification lies in the New World tropics, where twenty-four species belonging to thirteen genera, of which five are endemic, occur on ferns, *Araucaria*, palms, bromeliads and members of seventeen families of dicotyledons. North America does not appear to have contributed either to species- or host-diversity: its sole representative is a palmicolous species of *Hysterostomella* that has extended its range into Florida.

Africa plays host to ten genera (grouping twenty-four species) of which eight are shared with tropical America and two are endemic: *Perischizon* on Celastraceae* and Oleaceae in South Africa, and monotypic *Parmularopsella* on a member of the Burseraceae in Nigeria. The latter fungus, incidentally, is a segregate from the South American *Parmularia* from which it may not be generically distinct (Luttrell 1973). Of the taxa which Africa shares with the neotropics, one species occurs on ferns in West Africa and all the others are distributed in South and East Africa on members of one monocotyledonous family and seventeen dicotyledonous families. In Australia and New Zealand, eleven species belonging to seven genera have been recorded from ferns, southern conifers, Pandanaceae and representatives of five families of dicotyledons. Six of these genera are also present in both Africa and tropical America.

Twenty-three species of Parmulariaceae are known from tropical Asia and the East Indies. They belong to twelve genera of which four are endemic in the area. Their hosts range from ferns, palms, Pandanaceae, Flagellariaceae and Smilacaceae to the dicotyledonous Acanthaceae, Moraceae, Symplocaceae, Capparidaceae, Olacaceae, Rhamnaceae, Fagaceae, Rubiaceae, Juglandaceae, Convolvulaceae and Dilleniaceae -- an interesting mixture of plants apparently of both Gondwanalandian and Laurasian origin (Raven & Axelrod 1974). Of the eight Parmulariaceous genera that are not endemic to tropical Asia, seven occur both in tropical America and Africa, but only four in Australia, including *Aulacostroma*, which is not represented in Africa or America but has a species attacking *Pandanus* in Mauritius, India, the Philippines and Australia.

Clearly, the Parmulariaceae are a southern hemisphere group, possibly of West Gondwanaland origin. They are rare in areas north of the Tropic of Cancer, even where there is a climatic belt similar to that which they occupy in South Africa, south-east Australia, Tasmania and New Zealand. Their venture into the subtropical and temperate northern hemisphere is, as far as we know, limited to the palmicolous species in Florida, and *Parmulina* on *Daphniphyllum* in

---

* Families of angiosperms, throughout this paper are treated according to Willis (1973).

MAP 8.1: PARMULARIACEAE

(the number of host families for each genus is indicated by a numeral).

● on ferns

■ on southern conifers

○ on dicotyledons (Shown as outline as well as circle)

△ on monocotyledons

Genera: A. *Aulacostroma;* B. *Cocconia;* C. *Cycloschizon;* D. *Cyclostomella;* E. *Dothidasteroma;* F. *Ferrarisia;* G. *Hysterostomella;* H. *Inocyclus;* J. *Palawaniella;* K. *Parmularia;* L. *Parmulariopsis;* M. *Parmulariopsella;* N. *Parmulina;* O. *Perischizon;* P. *Polycyclina;* R. *Polycyclus;* S. *Pseudolembosia;* T. *Rhagadolobium;* U. *Rhipidocarpon;* V. *Symphaeophyma.*

MAP 8.2: CORYNELIACEAE

● on *Podocarpus* (Sections A. Afrocarpus; E. Eupodocarpus; N. Nageia; P. Polypodiopsis; S. Stachycarpus): 1. *Corynelia brasiliensis;* 2. *C. jamaicensis;* 3. *C. nipponensis;* 4. *C. oreophila;* 5. *C. portoricensis;* 6. *C. tropica;* 7. *C. uberata;* 8. *Lagenulopsis bispora;* 9. *Tripospora macrospora;* 10. *T. venezuelensis;* 11. *T. tripos;* 12. *Caliciopsis podocarpi.*

○ *Coryneliospora* on *Myrsine* (M) and *Rapanea* (R): 13. *C. fructicola;* 14. *C. rapaneicola.*

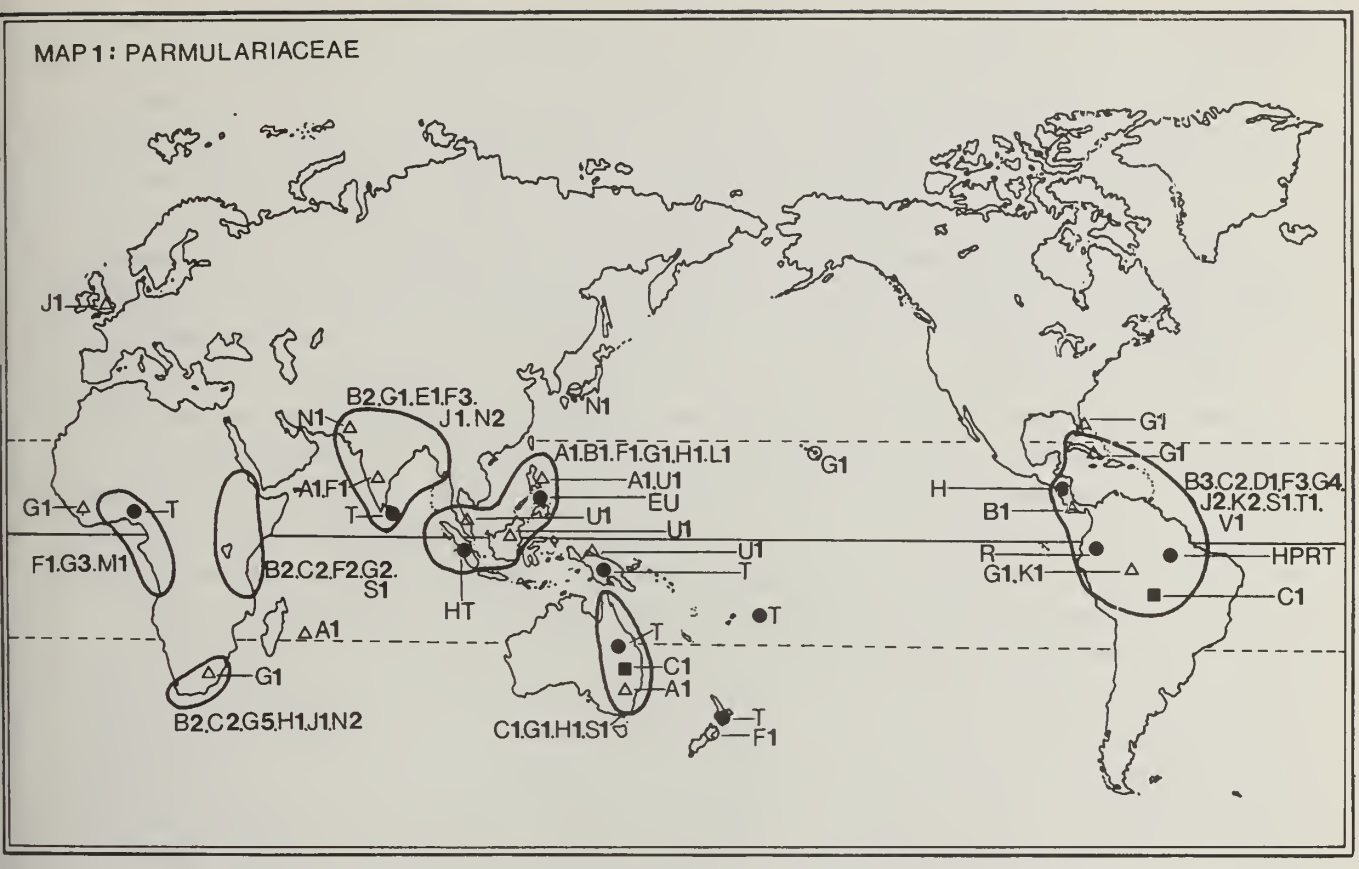
□ *Caliciopsis* on northern conifers and ectomycorrhizal trees: 15. *C. calicioides (Populus);* 16. *C. nigra (Juniperus);* 17. *C. orientalis (Acer);* 18. *C. pinea (Pinus);* 19. *C. pseudotsugae (Pseudotsuga);* 20. *C. subcorticalis (Quercus);* 21. *C. thujina (Chamaecyparis);* 22. *C. tiliae (Tilia)*■ on southern conifers: 23. *C. brevipes (Araucaria);* 24. *C. cochlearis (Pilgerodendron).*

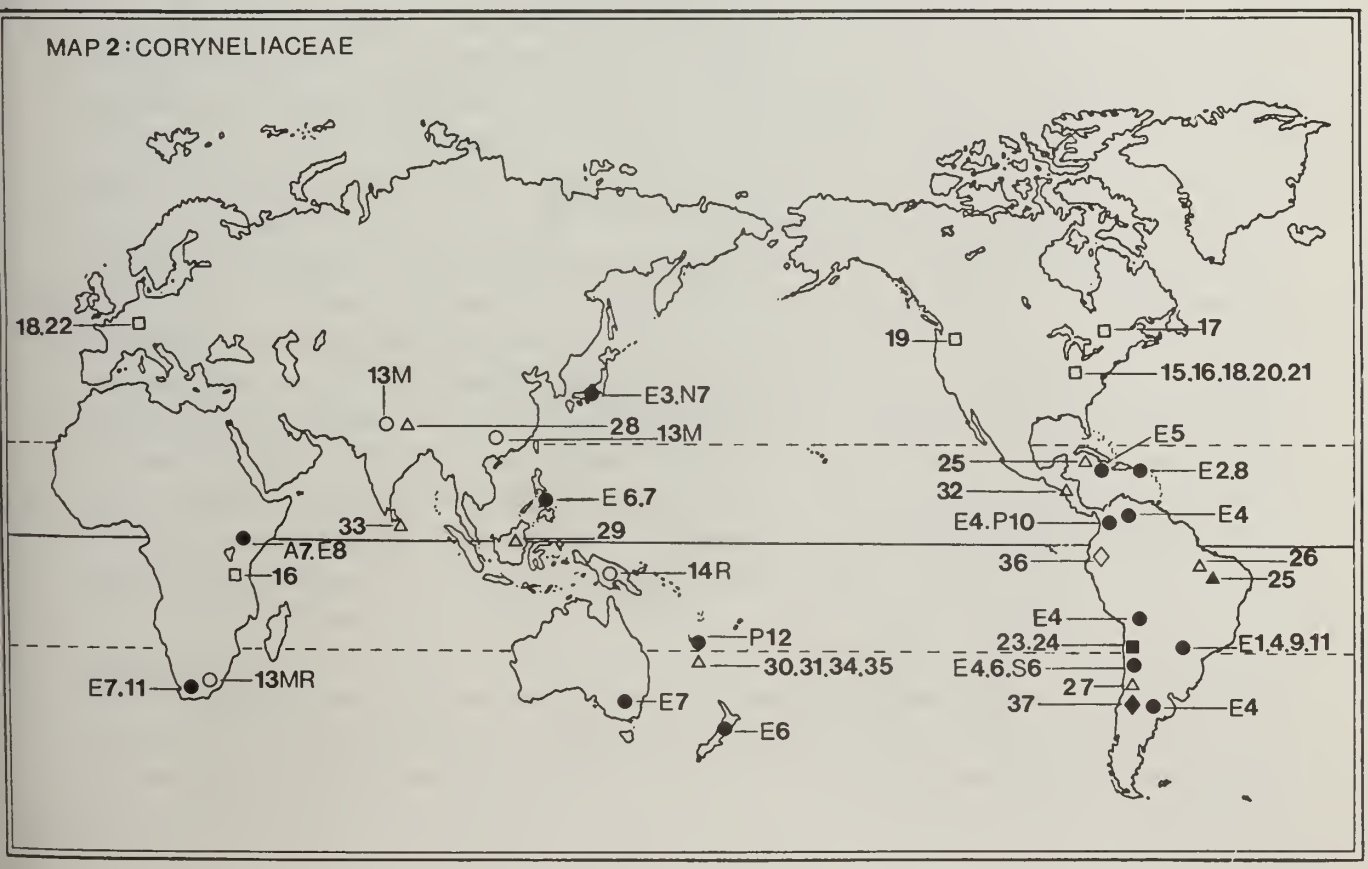
▲ on ferns: 25. *C. maxima (Polypodium).*

△ on other dicotyledons: 26. *C. arrhiza;* 27. *C. clavata (Drimys);* 28. *C. confusa (Myrsine);* 29. *C. elytranthicola (Elytranthe);* 30. *C. myrticola (Myrtus);* 31. *C. rapaneae (Rapanea);* 32. *C. struthanthi (Struthanthus);* 33. *C. symploci (Symplocos);* 34. *C. veillonii;* 35. *C. xanthostemonis (Xanthostemon).*

◇ 36. *Corynelia sydowii (?Eugenia)*

◆ 37. *Coryneliopsis antarctica (Cyttaria* on *Nothofagus)*


MAP 1: PARMULARIACEAE
J1
B2.G1.E1.F3.
J1.N2
N1
N1
A1.B1.F1.G1.H1.L1
A1.U1
EU
U1
U1
U1
T
G1
A1.F1
T
G1
T
F1.G3.M1
B2.C2.F2.G2.
S1
HT
A1
G1
B2.C2.G5.H1.J1.N2
T
C1
A1
C1.G1.H1.S1
T
F1
G1
G1
H
B1
B3.C2.D1.F3.G4.
J2.K2.S1.T1.
V1
R
G1.K1
HPRT
C1


MAP 2: CORYNELIACEAE
18.22
13M
E3.N7
28
13M
E 6.7
33
29
A7.E8
16
14R
P12
30.31.34.35
E7.11
13MR
E7
E6
19
17
15.16.18.20.21
E5
25
E2.8
32
E4.P10
E4
36
26
25
E4
23.24
E1.4.9.11
E4.6.S6
27
37
E4

Japan, to *Palawaniella* on *Ammophila* in an enigmatic record from Britain, and to species on Laurasian hosts in the Himalayan regions characterized by disharmonic floras.

Though most of the genera are shared by the three southern continents, all species there are vicariant*. They occur on different host families on different continents except for the plants parasitized by species of *Hysterostomella* and *Pseudolembosia*. *Hysterostomella* species occur on Dilleniaceae (*Tetracera*) in South America, Africa, south-east Asia and Australia, on Apocynaceae in South America and Africa, and Oleaceae in South Africa and Hawaii; and *Pseudolembosia* species occur on Myrtaceae in South America and Australia, and -- in what is undoubtedly a recent introduction -- on *Eucalyptus* in East Africa. This general, though vicariant, distribution of the family in the southern hemisphere indicates a habitation of long standing.

To reach some understanding of this pattern of distribution, we must look at the geological history of the regions in which these fungi occur today and might have occurred in earlier times. For our discussion, we shall accept the recent view of plate tectonics and continental drift as outlined by Schuster (1976). Africa-Madagascar is seen as splitting away from southern Gondwanaland in the early Cretaceous period some 135 million years before the present (m.y.B.P.), through the opening of the South Atlantic; but Africa's tropical west remained more or less connected to its West Gondwanaland partner, South America, until after mid-Cretaceous times some 90 m.y.B.P. Evidence is presented by Schuster for the postulation that India left East Gondwanaland later than is generally assumed, around the mid-Cretaceous, with archipelagic connections retained for some 20 m.y., its migration ending at its present Laurasian port as recently as 40-45 m.y. ago. New Zealand became isolated about 80 m.y. ago. The Antarctic connection between South America and Australia was maintained until well into the Tertiary, about 45-50 m.y.B.P., but for about the last 20 m.y. of that period the accumulating ice in the Antarctic uplands restricted passage between those continents to only cold-adapted organisms. Australia's migration (with a part of New Guinea) began about 40 m.y. ago, ending around 10-12 m.y.B.P. with the formation of Wallace's Line at the point of collision between the Australasian Plate and Malaysian Laurasia. It is in the light of this postulated tectonic activity that we shall now look at the geographic distribution of the Parmulariaceae.

The key to the distribution of the Parmulariaceae in Asia and their strong West Gondwanalandian connection would seem to be India, whose migration across the Indian Ocean is now accepted as geological fact. It is a distribution that lends support to Schuster's (1976) contention that the breakaway Indian plate left Gondwanaland only after the mid-Cretaceous, at a time when angiosperms were already widespread and highly diversified. It can be presumed that, during fifty million years of migration, the floral composition of the Indian 'raft' would have changed drastically, with the loss especially of cool-adapted passengers. Evidence exists for the elimination of certain groups of austral gymnosperms that were present in India in the early Cretaceous (Florin 1963). Parmulariaceous fungi strengthen this evidence: *Cycloschizon*, species of which are parasitic on conifers both in South America and in Australia, is not found on conifers in Asia. But primarily warm-adapted Parmulariaceae parasitic on angiosperms appear to have fared well. South-central Asia (Pakistan, India, Sri Lanka and Burma) has no endemic

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* Vicariance is here taken in the broad sense to cover the phenomenon of the establishment of descendant taxa through isolation of parental populations (Löve 1955, Croizat et al. 1974).

genera. With the exception of the species of *Aulacostroma* already mentioned, all eight species in this region, belonging to the six genera shared with West Gondwanaland, are vicariant, and -- again with the exception of *Aulacostroma* -- all eight have achieved host vicariance. When the Indian 'raft' docked, some 45 m.y.B.P., and its depleted, insular biota became invaded by Laurasian elements, nearly all surviving members of the Parmulariaceae 'jumped' to Laurasian or more recently evolved hosts, for we find *Cocconia* on Symplocaceae, *Cycloschizon* on Olacaceae, *Ferrarisia* on Smilacaceae, Rhamnaceae and Convolvulaceae, *Palawaniella* on Fagaceae, and *Parmulina* on Smilacaceae and Juglandaceae. Their subsequent dispersal eastward is seen in the sympatry of Asian mycota: *Cocconia spurcaria* on Moraceae in Sri Lanka, the Philippines and Sarawak, *Ferrarisia ipomoeae* on Convolvulaceae in India and the Philippines, and *Parmulina exulpta* on three members of the Euphorbiaceae in Sri Lanka, Malaya and the East Indies.

The distribution of the Parmulariaceae in the East Indies indicates a southward spread from south-east Asia rather than northward from Australia. Again, the southward spread is the direction postulated for angiosperms by Schuster (1976), who contends that the Australian plate (with the southern part of New Guinea) would have been biotically depauperate as it approached the East Indies late in the Tertiary, and thus in a better position to receive than to give. However, as far as the Parmulariaceae are concerned, there has been no transgression of Wallace's line, except for the endemic taxa that arose in the Malaysian melting pot of Laurasian and Gondwanalandian floras, especially *Rhipidocarpon*, which occurs on *Nypa* in Malaya, the Philippines, Borneo and New Guinea. It is true that the distribution of Parmulariaceae on ferns, especially of nine vicariant species of *Rhagadolobium*, extends from Sri Lanka, Java, and the Philippines through to New Guinea, Australia, New Zealand and Samoa, but they also occur in Brazil and Nigeria -- on continents linked only until some 90 m.y. ago.

Returning to the starting premise which we are endeavouring to test, i.e., that the antiquity of the host reflects that of its parasites and vice versa, we must focus on the parasites of ferns and austral gymnosperms. The absence of Parmulariaceae on cryptogamic and gymnospermous hosts in southern and eastern Africa points to the absence of the parasites there at the time of the opening of the south Atlantic about 130 m.y.B.P., and their subsequent invasion of the continent with their angiospermous hosts using alternative routes (perhaps from tropical South America, because *Parmularia-Parmulariopsella*, now in Brazil and Nigeria, may have once had continuous distribution). On the other hand, assuming that the Parmulariaceae were always adapted to warm climates, an origin prior to 60 m.y.B.P. is indicated if overland migration between South America and Australia is a necessary explanation for the step-wise movement of the host together with its specific but not systemic foliicolous parasite, a combination with limited means of dispersal. An even earlier existence, 80 and 90 m.y.B.P., must be envisaged to account for the presence of pteridicolous species in New Zealand and West Africa.

The Coryneliaceae

The family consists of six genera, of which three, with twelve species, occur in the southern hemisphere and east Asia (Map 8.2). Eleven of those species are parasitic on leaves of *Podocarpus*, and the twelfth was found on an undetermined host, apparently *Eugenia*. The greatest diversity of species is found in the neotropics where podocarps play host to five out of

seven species of *Corynelia*, two of three species of *Tripospora*, and a sole representative of *Lagenulopsis*. Two of the species occur elsewhere: *Lagenulopsis bispora* is found in East Africa, and the Chilean *Corynelia tropica* is known from New Zealand and the Philippines. In the Old World, one species of *Tripospora* is confined to South Africa, a *Corynelia* to Japan, and the remaining species, *C. uberata*, occurs in South and East Africa, Australia, New Zealand, the Philippines and Japan.

Podocarpus, the largest genus of austral conifers, is credited with an origin in terminal Palaeozoic to early Mesozoic times (Buchholz & Gray 1948), with subsequent diversification into geographically separated sections of vicariant species following the complete segmentation of Gondwanaland in the late Mesozoic (Gray 1969). The section *Eupodocarpus** is widely distributed in the southern hemisphere and extends into south-east Asia, and this section is of particular interest to us because it provides most of the hosts for the Coryneliaceae. If, on account of its wide distribution, *Eupodocarpus* is taken to be the oldest section, and if the Coryneliaceae have co-evolved with its members (as they appear to have done), we could postulate the origin of the parasites before the break-up of Gondwana at the start of the Jurassic, 180-200 m.y.B.P. This line of reasoning is contradicted by the pattern of vicariance (as interpreted by Cracraft 1975) within the genus, and by the relatively advanced anatomical features of *Eupodocarpus* (Buchholz & Gray 1948), both of which point to *Eupodocarpus* as the most recently evolved section. We are, therefore, faced with the problem of a preferential dispersal of this relatively recent group of podocarps across the southern hemisphere and to (or from) south-eastern Asia since the mid-Mesozoic. But postulation of a long-range dispersal of host seeds, etc., by birds or other agencies does not satisfactorily account for the coinciding spread of their obligate and specific fungal parasites. Therefore, we must consider the possibility of overland migration of host and parasite together, first via the Antarctic land bridge (between South America and Australia), then through passive rafting on India, and a subsequent eastward dispersal during the Tertiary in Asia, where some of the Coryneliaceae make a 'jump' to members of the section *Nageia* of *Podocarpus*. Perhaps the fungi are better indicators of the age of *Eupodocarpus* than other pieces of evidence currently used to date the section, because the diversified mycota of the Coryneliaceae on *Eupodocarpus*, as well as on the reputedly more ancient endemic sect. *Afrocarpus* in southern and eastern Africa, appears to reflect a situation established prior to the opening of the south Atlantic 120-135 m.y.B.P.

The Coryneliaceae that remain to be considered are two species of *Coryneliospora*, occurring on fruits of *Myrsine* and *Rapanea* in South Africa, New Guinea, the Himalayas and China, and *Caliciopsis* with twenty-two species: five in New Caledonia on *Podocarpus*, *Myrtus*, *Rapanea* and *Xanthostemon*, one on *Elytranthe* in North Borneo, three in Chile on *Araucaria*, *Pilgerodendron* and *Drimys*, three in tropical America on *Polypodium* and *Struthanthus*, one on *Symplocos* in Sri Lanka, one on *Myrsine* in Nepal, and eight on northern conifers (mainly Pinaceae), *Populus*, *Quercus* and *Tilia* in temperate North America and Eurasia. Although *Coryneliospora* and *Caliciopsis* have departed considerably in morphology from their podocarpicolous relatives, their

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* i.e., *Podocarpus* sect. *Podocarpus*. Although Art. 21 of the ICBN rejects the use of the prefix "Eu-" in formal designation of the type section of a genus, we adopt its use here informally for the sake of convenience.

geographical distribution and the accepted antiquity of their hosts leads to the conclusion that they were long-established in Gondwanaland before being dispersed to Asia. The apparently once wide distribution of *Caliciopsis* in the northern hemisphere, broken into its present-day discontinuity by Pleistocene glaciation, also indicates late Mesozoic diversification. Yet, if *Caliciopsis* reached the northern hemisphere in the late Mesozoic, as its present host range suggests, neither the Indian 'raft' nor the Central American 'filter' is a convincing dispersal-route from the chronological and geological points of view, respectively. If the Coryneliaceae are as old as their association with podocarps in the southern hemisphere indicates, we should perhaps consider the present occurrence of dominant, highly vicariant taxa in the two hemispheres as representing descendant mycotas from Triassic or early Jurassic Pangaean ancestors.

The Phacidiales

This order is usually treated as a heterogeneous assemblage of three families which may not be closely related phylogenetically: the Phacidiaceae, the Cryptomycetaceae and the Rhytismataceae (sensu Korf 1973, or Hypodermataceae, sensu Darker 1967). The Phacidiales conjure up a picture of a north temperate and boreal group, but the numerous exceptions that exist undermine the credibility of this generalization. To determine the extent to which the exceptions obscure patterns of distribution or, indeed, whether non-random patterns exist at all, it is necessary to take a closer look at the host range and mycogeography of individual members of the three families (Maps 8.3 & 8.4).

The Phacidiaceae comprise nine genera of which two, on vascular cryptogams, may be of considerable antiquity: *Phacidina* grows on *Lycopodium*, and *Cryptomycina* on *Osmunda* and *Pteridium*. However, despite the cosmopolitanism of their hosts, the parasites are found only in cool-temperate Eurasia and North America. They share the same niche with other members of the family that are adapted to ecologically associated host plants: *Therrya, Micraspis, Phacidium, Pseudophacidium* and *Lophophacidium* occur mainly on the Pinaceae (*Abies, Picea, Pinus*) and other, mostly ectomycorrhizal or ericaceous, Laurasian plants such as *Betula, Quercus, Salix, Gaultheria, Ledum, Calluna, Rhododendron, Vaccinium, Juniperus, Empetrum* and *Ilex*. Their habitat is the boreal and cool-temperate zone and its climatic and floristic extensions and disjunctions as far south as the montane areas of Pakistan and Malaya (*Phacidium* and *Therrya* on *Pinus, Neophacidium* on *Quercus*), and India (*Phacidium* on *Quercus* and *Holostemma, Pseudophacidium* on *Photinia*). The only species of the Phacidiaceae that do not conform to the Laurasian pattern are a *Phacidium* that occurs in South Africa on a member of the ancient West Gondwanalandian Chrysobalanaceae, and in Australia on *Eucalyptus*, and *Neophacidium* on *Gynoxys* (Compositae) in South America. However, the latter may be discountable as a significant exception, because *Neophacidium* is only a slightly distinguishable segregate from *Phacidium*, and its host seems to be (Raven & Axelrod 1974) of relatively recent, mid-Oligocene origin in northern South America.

The Cryptomycetaceae do not occur on hosts older than the Pinaceae (*Potebniamyces* on *Pinus, Pseudotsuga* and *Tsuga*) or *Salix (Cryptomyces)*. Other species of *Potebniamyces* inhabit the originally Gondwanalandian but now predominantly north-temperate Rosaceae, and *Pseudorhytisma* the Polygonaceae. A *Cryptomyces* species of disjunct distribution is found on *Salix* and

PHACIDIALES (Maps 8.3 & 8.4)

(Distribution north of the Tropic of Cancer generalized on the basis of selected records from literature and Herb. IMI).

- ◆ on *Lycopodium* (L) and *Equisetum* (E)
- ● on ferns
- ■ on endomycorrhizal conifers: *Cunninghamia, Sequoia* (S), *Pilgerodendron* and *Podocarpus* (P), and *Dacrydium* (D).
- □ on ectomycorrhizal conifers: *Juniperus* (J) and Pinaceae.
- ○ on Ericaceae
- ◇ on ectomycorrhizal dicotyledonous trees (E; *Eucalyptus*)
- ▲ on grasses
- △ on other dicotyledons and monocotyledons (C; *Cocos*; M; *Manifera*).

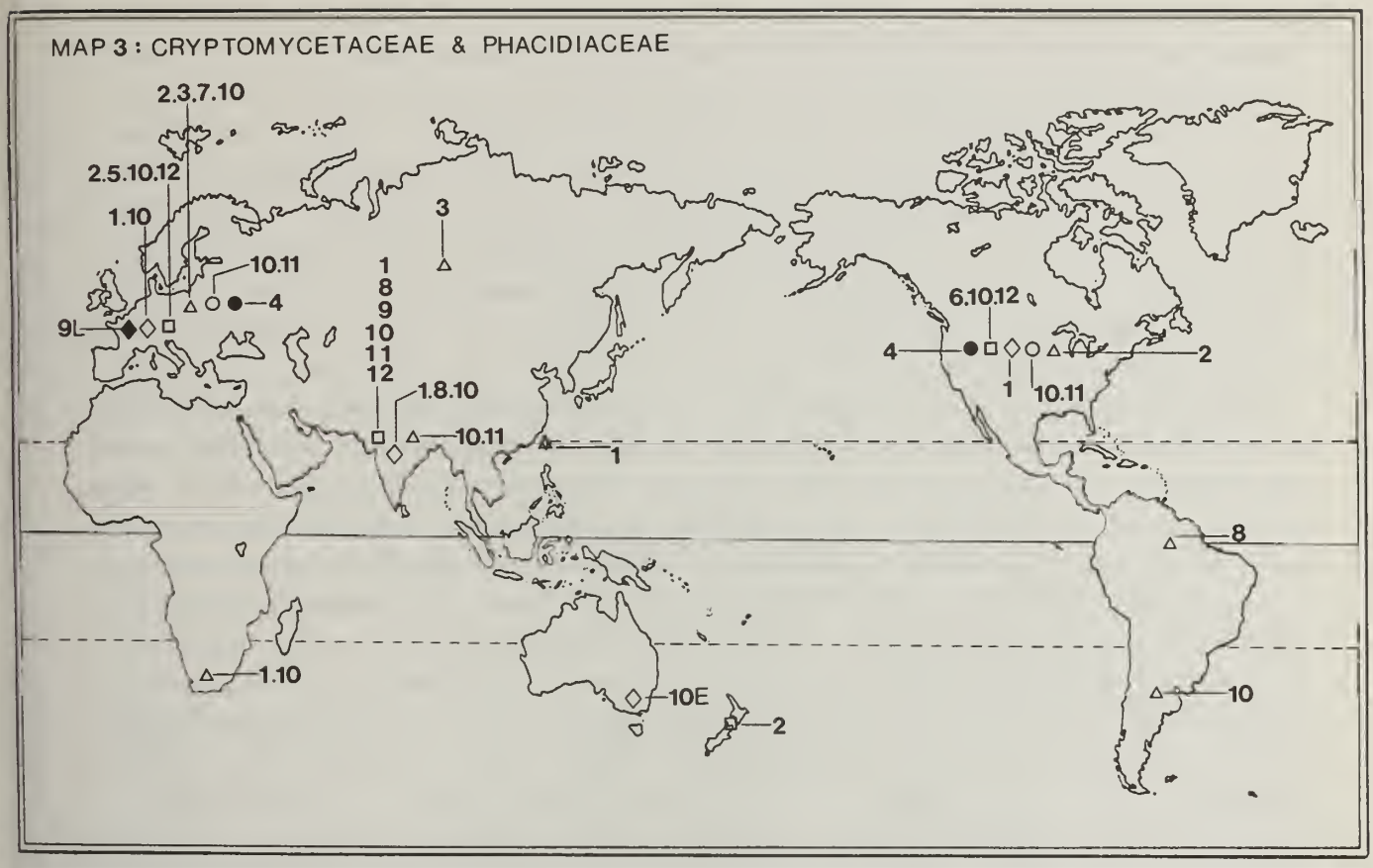
MAP 8.3: CRYPTOMYCETACEAE AND PHACIDIACEAE

Cryptomycetaceae: 1. *Cryptomyces;* 2. *Potebniamyces;* 3. *Pseudorhytisma.*

Phacidiaceae: 4. *Cryptomycina;* 5. *Lophophacidium;* 6. *Micraspis;* 7. *Nannfeldtia;* 8. *Neophacidium;* 9. *Phacidina;* 10. *Phacidium;* 11. *Pseudophacidium;* 12. *Therrya.*

MAP 8.4: RHYTISMATACEAE

1. *Bifusella;* 2. *Bifusepta;* 3. *Ceratophacidium;* 4. *Coccomyces;* 5. *Colpoma;* 6. *Davisiomycella;* 7. *Duplicaria;* 8. *Elytroderma;* 9. *Hypoderma;* 10. *Hypodermella;* 11. *Isthmiella;* 12. *Lirula;* 13. *Lophodermella;* 14. *Lophodermina;* 15. *Lophodermium* (and *Lophodermellina*); 16. *Lophomerum;* 17. *Meloderma;* 18. *Nymanomyces;* 19. *Placuntium;* 20. *Ploioderma;* 21. *Rhytisma;* 22. *Soleella;* 23. *Virgella.*


MAP 3 : CRYPTOMYCETACEAE & PHACIDIACEAE
2.3.7.10
2.5.10.12
1.10
10.11
4
9L
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1
8
9
10
11
12
1.8.10
10.11
1
6.10.12
4
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10.11
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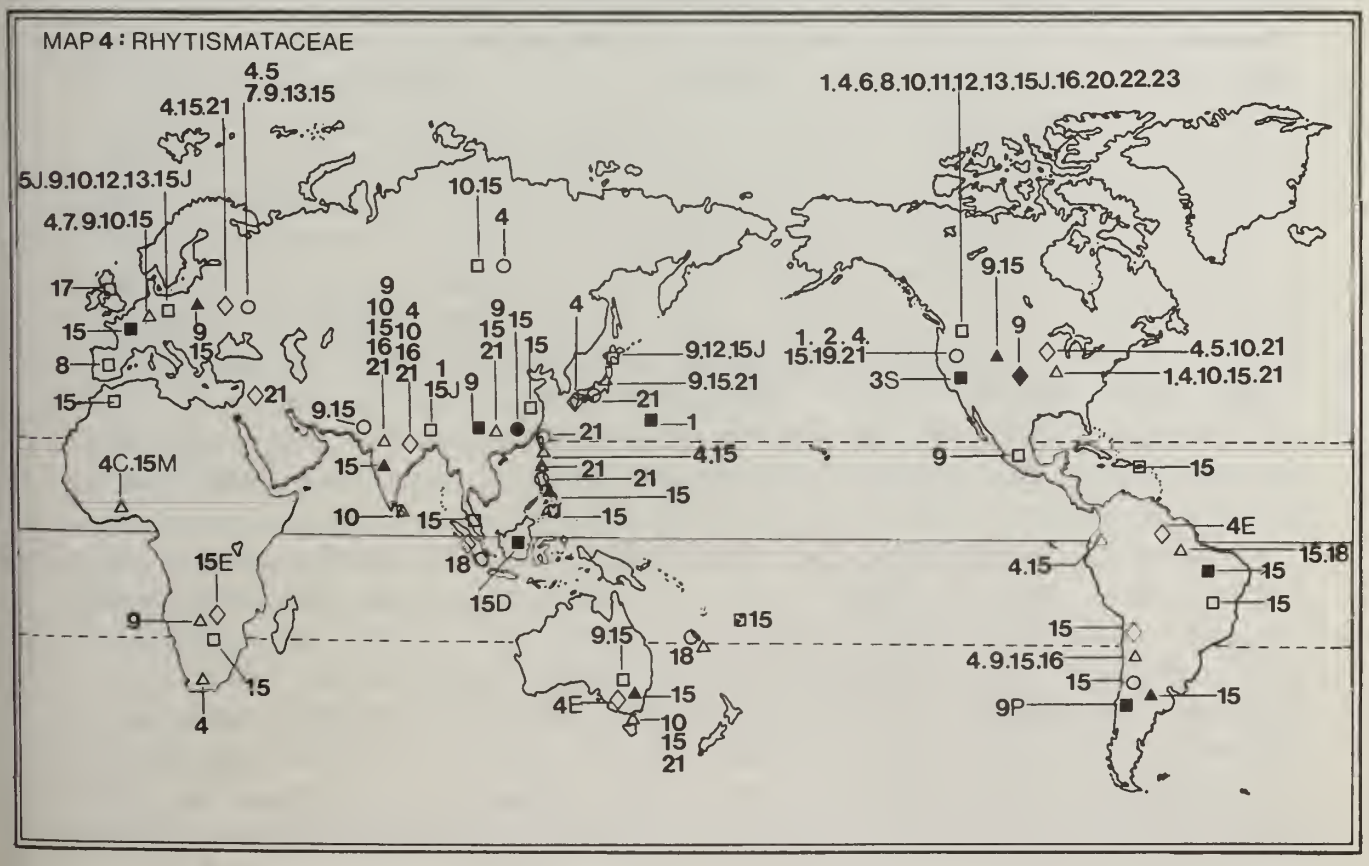
1.10
10E
2
10


MAP 4 : RHYTISMATACEAE
4.5
7.9.13.15
4.15.21
5J.9.10.12.13.15J
4.7.9.10.15
17
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15
21
4C.15M
15E
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4
10.15
4
9
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15
16
21
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16
21
1
15J
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9.15
15
10
15
18
15D
9
15
21
15
15
4
9.12.15J
9.15.21
21
1
21
4.15
21
21
15
15
9.15
18
15
4E
10
15
21
1.4.6.8.10.11.12.13.15J.16.20.22.23
9.15
1. 2. 4.
15.19.21
3S
9
4.5.10.21
1.4.10.15.21
9
15
4E
15.18
4.15
15
15
15
4.9.15.16
15
9P
15

Quercus in India, another in South Africa on a recent Laurasian immigrant, *Myrica*, and *Potebniamyces*, presumably guided by man, has accompanied *Cedrus* to New Zealand.

The Rhytismataceae, a much larger family, has a much wider distribution. In fact, its species occur on every continent and on plants of both Gondwanalandian and Laurasian origin and, at first sight, appear to have diversified sufficiently to obscure their original distribution patterns. This is not completely true. The largest concentration of genera, in fact all but one genus, is in boreal and cool-temperate Eurasia and North America. The one exception is the atypically dark-spored and taxonomically poorly defined *Nymanomyces*, a complex of five species found in the Old World tropics, but -- significantly -- mainly on Laurasian hosts such as *Acer*, *Lonicera*, *Rhododendron* and *Symplocos*.

In the cool-temperate northern hemisphere, the Rhytismataceae are most abundant on Pinaceae, but also occur on Cupressaceae and Taxodiaceae, on northern ectomycorrhizal Amentaceae (Betulaceae, Fagaceae, and Salicaceae) and their ecological neighbours: the Ericaceae (Rhododendroideae and Vaccinioideae, both Laurasian according to Aubréville 1974), Laurasian Aceraceae, as well as Cyperaceae, Juncaceae and Typhaceae, and odd members of Laurasian Liliaceae, Paeoniaceae, Aquifoliaceae (*Ilex*), and the originally Gondwanalandian but now chiefly northern Araliaceae, Vitaceae, Linaceae and Rosaceae. The occurrence of the Rhytismataceae in the tropics and southern temperate zone seems to be mainly the result of the extensions or isolation of northern fungus taxa along with their hosts: *Acer*, *Betula*, *Quercus*, *Viburnum*, *Lonicera*, *Lagestroemia*, *Rhamnus* and *Ilex* in India and Hong Kong; *Paeonia*, *Quercus* and *Hedera* in Pakistan; *Viburnum* and *Ilex* in the Philippines; *Pinus* in India, Pakistan, Malaya and the Philippines; and *Fagus* and *Veronica* in South America. Man has also played his role in dispersing pinicolous species to Australia, East Africa, Fiji, South America and the West Indies.

A smaller group of the Rhytismataceae, consisting of some species of *Hypoderma* and *Lophodermium*, occurs on a large number of widely distributed gramineous hosts that include *Agropyron*, *Ammophila*, *Arundinaria*, *Phragmites* and *Stipa* in North America and temperate and subtropical continental Eurasia, *Saccharum* in the Philippines, *Spinifex* and *Sporobolus* in Australia, and *Festuca*, *Luzula* and *Poa* in South America. Grasses are a late Cretaceous or early Palaeogene development, and although their ancestral tribes may have been present in Gondwanaland prior to its splitting, the present-day vicariant distribution of the Gramineae into seven provinces indicates a definite post-continental-drift pattern (Clayton 1975). The seven provinces are Eurasia, North America, temperate South America, tropical South America, Africa, Australia, and India and Indomalaysia. Little or no overlap in the distribution of grasses exists anywhere except among the three New World provinces; and it is here, in South America, where the continuity of their hosts is uninterrupted, that the strong representation of graminicolous Rhytismataceae occurs.

There remains a group of exceptional records of Rhytismataceous species that belong to three northern genera but do not show obvious links (either of host or geography) with their northern relatives: a *Hypoderma* on *Richea* in Australia and on *Podocarpus*, *Pilgerodendron*, *Berberis* and *Rubus* in South America; *Coccomyces* on *Clusia*, *Inga*, *Eryngium*, *Eucalyptus* and a member of the Lauraceae in South America, and on *Eugenia* and *Cocos* in Africa and *Eucalyptus* in Australia; and *Lophodermium* on *Dacrydium* in Borneo, on *Clusia*, *Cryptocarya*, *Boldoa* and *Geuvina* in South America, on *Mangifera* in India and Guinea, and on *Eucalyptus* in Malawi. If we discount the lines of dispersal for which man himself is likely to be responsible (*Cocos* and *Mangifera* in West

Africa, *Cunninghamia* in South America, *Eucalyptus* in Africa and South America), and also depreciate the occurrence of the parasites on hosts of Laurasian origin or predominantly present-day distribution (*Berberis, Eryngium, Rubus*) and hosts of relatively recent history (*Richea*), we are still left with a group of species occurring on mostly old Gondwanalandian plants: *Podocarpus, Pilgerodendron, Clusia, Inga, Boldoa* and *Geuvina* in South America, *Combretum* and *Eugenia* in Africa, *Dacrydium* in Borneo, and *Eucalyptus* in Australia. How, then, do we see the history of this group from its present-day distribution?

The presence of the same or vicariant species of the Rhytismataceae in both North and South America poses the question of whether their dispersal into the temperate southern hemisphere could have been along the "marsupial route" postulated by Schuster (1976) to explain the direct migration of marsupials, *Nothofagus* and, possibly, *Araucaria*, from North America to Australia via South America and Antarctica. According to this scenario, *Nothofagus* reached New Zealand in the late Cretaceous and Australia in early Tertiary, i.e., after the separation of both Africa and India from Gondwanaland. The Rhytismataceae are not known to occur on *Nothofagus* despite its suitability for fulfilling the preferences of the parasite for a host that is cool-adapted, gregarious, evergreen and ectomycorrhizal. If the Rhytismataceae had occurred on *Nothofagus* at the time it inhabited North America, there would seem to be no reason for the elimination of the fungi if the host could survive the migration southward. We must conclude that the Rhytismataceae did not occur on *Nothofagus* in its early history, and that, therefore, this group of parasites is likely to be younger than 80 m.y. Furthermore, since the Antarctic connection remained open to the migration of cool-adapted plants until some 45 m.y.B.P., it appears that parasites of the circumantarctic *Geuvina, Rostkovia* and *Pernettya* would have been able to leave South America with their hosts along that route. From the absence of Rhytismataceae in the then expanded distribution of these plants, we can only conclude that the Rhytismataceae developed no earlier than the late Cretaceous, if not even more recently. And their dispersal into the southern hemisphere and onto Gondwanaland plants was not via the central American 'filter' that, according to Schuster (1976), remained operational only until mid-Cretaceous times, but independently through much more recently re-established routes: the central American isthmus and the Andean 'spine' available since 4.7 m.y.B.P., the Euro-African link re-established 17 m.y.B.P., or the collision between Australian and Asian plates of 10-12 m.y. ago.

The same pattern may apply to the Phacidiaceae and the Cryptomycetaceae. The Phacidiaceae, despite the occurrence of some of their members on plants of great antiquity, have a very restricted geographical distribution, showing no sign of an early existence in an area much broader than their present range. And the Cryptomycetaceae -- adapted to the cortical tissues of woody, mainly ectomycorrhizal plants with which they appear to have co-evolved -- must have become separated from any austral relatives by the tectonic events of the late Mesozoic and climatic differentiation in the Palaeogene.

The "sooty-mould" complex

Any speculation on the origin of pleomorphism in Ascomycetes must include consideration of the sooty moulds, because some of the most dramatic examples of this phenomenon of anamorphic diversity are to be found in this complex of fungi. The sooty moulds, as defined by Hughes (1976), include unitunicate Triposporiopsidaceae, and bitunicate Chaetothyriaceae, Antennular-

SOOTY MOULDS (Maps 8.5 & 8.6)

- ● on ferns and southern conifers
- □ on northern conifers
- ■ on Pinaceae
- ○ on arctic-alpine angiosperms (mainly Ericaceae).
- △ on other dicotyledons
- ▲ on monocotyledons
- ◇ on northern ectomycorrhizal trees

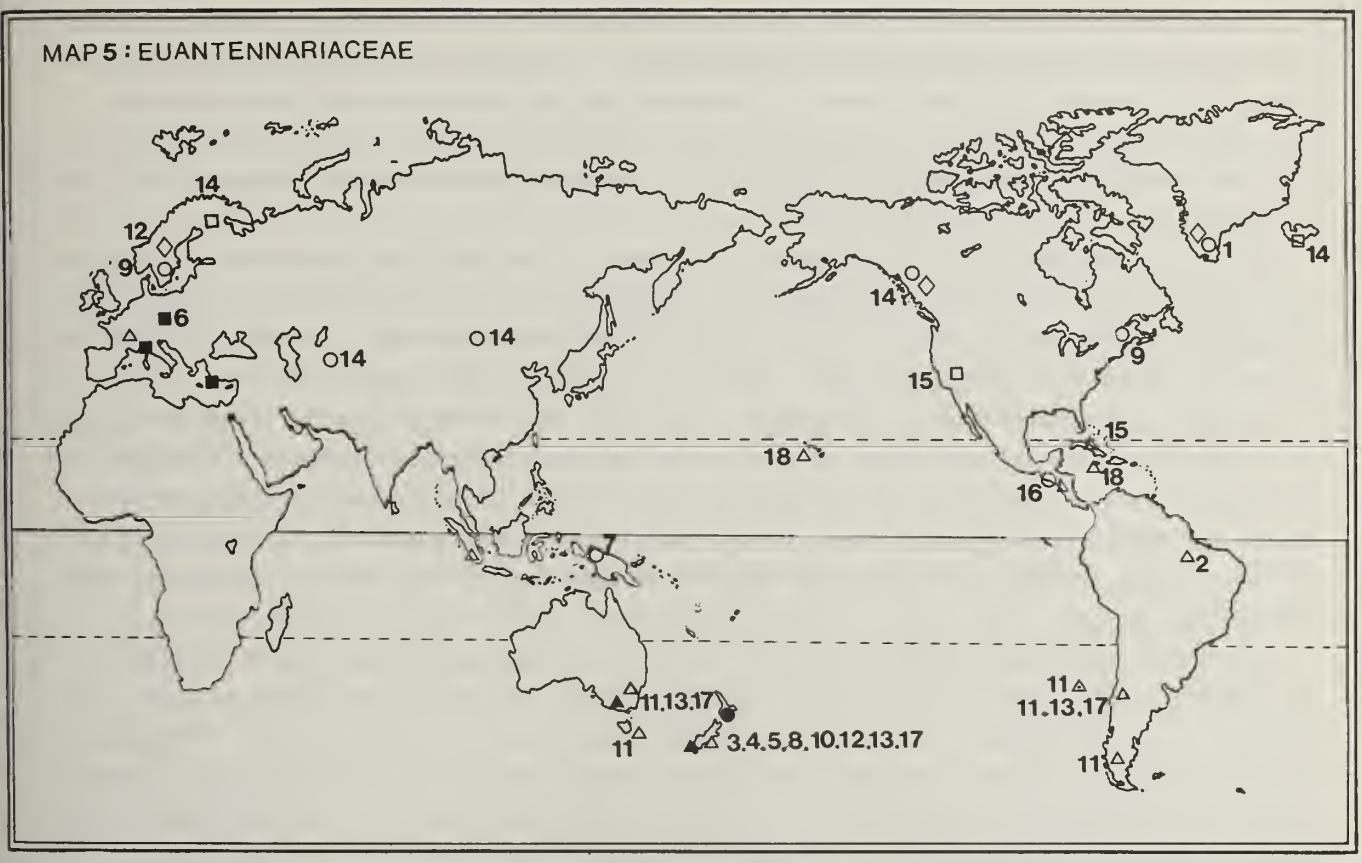
MAP 8.5: EUANTENNARIACEAE

1. *Antennatula arctica;* 2. *A. atra;* 3. *A. dingleyae;* 4. *A. fisherae;* 5. *A. fraserae;* 6. *A. pinophila;* 7. *A. shawiae;* 8. *A. triseptata;* 9. *Euantennaria arctica;* 10. *E. caulicola;* 11. *E. mucronata;* 12. *E. novae-zealandiae;* 13. *E. pacifica;* 14. *E. rhododendri;* 15. *E. spongiosa;* 16. *E. tropicicola;* 17. *Trichopeltheca asiatica;* 18. *T. stevensii.*

MAP 8.6: METACAPNODIACEAE

1. *Capnobotrys dingleyae;* 2. *C. neesii;* 3. *Capnocybe fraserae;* 4. *C. novae-zealandiae;* 5. *C. spongiosa;* 6. *Metacapnodium dennisii;* 7. *M. juniperi;* 8. *M. quinqueseptata;* 9. *Ophiocapnocoma batistae;* 10. *O. phloiophila.*

Unpublished records of Euantennariaceae and Metacapnodiaceae are included.


MAP 5 : EUANTENNARIACEAE
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11.13.17
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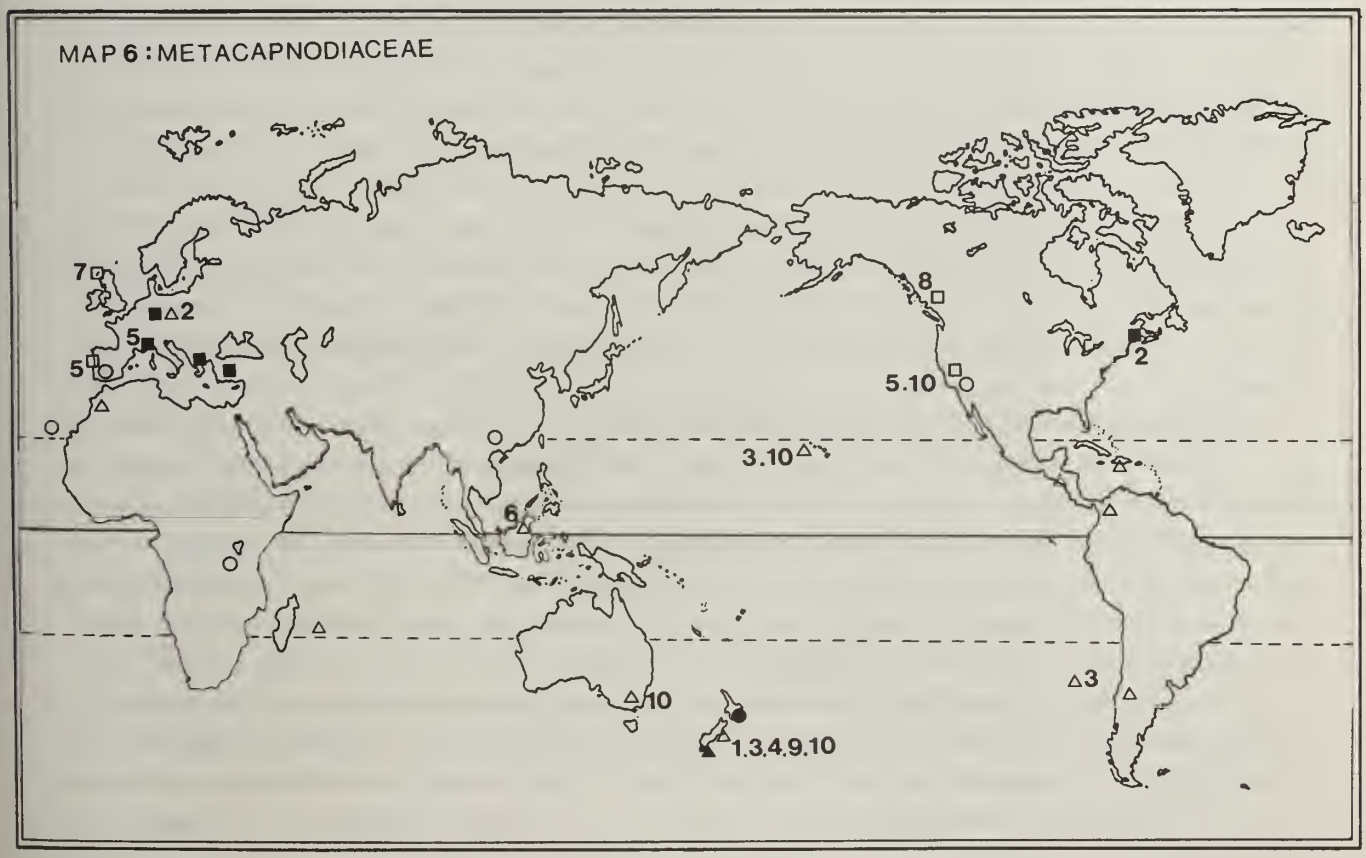
3.4.5.8.10.12.13.17
11
11.13.17
11


MAP 6 : METACAPNODIACEAE
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5.10
3.10
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1.3.4.9.10

iellaceae, Seuratiaceae, Capnodiaceae, Metacapnodiaceae and Euantennariaceae. At our present level of familiarity with the group, it is premature to speculate on the geographic past of sooty moulds generally, with the exception, perhaps, of the Metacapnodiaceae and the Euantennariaceae. These two families have received much of Hughes's attention during the past fifteen years and, as a result of his studies, their taxonomic circumscription, pleomorphism and geographic distribution are better known.

The Metacapnodiaceae and the Euantennariaceae occur in cool-temperate or montane evergreen hygrophytic forests as saprobes on resins or sugar-exudates of sap-sucking insects. Their association is, therefore, with insects, mainly coccids, rather than with specific plants. However, in many cases, the identity of the associated insect is not known, and our acquaintance with the frequency and specificity of the relationship is fragmentary in the extreme. It is not the purpose of this paper to pursue this interesting and possibly revealing aspect of fungus-insect co-evolution, beyond assuming that the kind, diversity and distribution of plants bearing sooty moulds must be to some extent related to the kind, diversity and distribution of their honeydew-producing pests; and for this reason we focus on plant substrates in this consideration.

To begin with the Euantennariaceae (Map 8.5): four out of eight known species of *Euantennaria* and four out of eight species of *Antennatula* occur in New Zealand on ferns, austral conifers and Gondwanalandic angiosperms, both monocotyledonous and dicotyledonous. Three of the New Zealand species of *Euantennaria* are also found in south-eastern Australia on monocotyledons and dicotyledons, and the same three species occur in south-western South America on dicotyledons. A different species of *Euantennaria* and an *Antennatula* are associated with Ericaceae and dicotyledonous trees in Central and South America; and there is also an alpine ericaceous *Antennatula* in the Indonesian part of New Guinea. In the boreal regions of the northern hemisphere, *Euantennaria arctica, E. rhododendri* and *Antennatula arctica* are associated with the Ericaceae, *Juniperus* and ectomycorrhizal dicotyledonous trees in Scandinavia, Siberia, Alaska, eastern Canada (Gaspé) amd Greenland; *Euantennaria spongiosa* occurs on *Libocedrus* in California, and *Antennatula pinophila* grows on pines in central Europe. The distribution of both species of *Trichopeltheca* is similar. *T. asiatica* is associated with a wide range of indigenous plants in New Zealand, but only with dicotyledons in south-east Australia and western South America, and *T. stevensii* is found on dicotyledons in Hawaii and the West Indies.

The greatest diversity of the Metacapnodiaceae (Map 8.6) is also in New Zealand, where two out of three known species of *Capnocybe*, one of two of *Capnobotrys*, and both species of *Ophiocapnocoma* occur on ferns, austral gymnosperms, and also both monocotyledonous and dicotyledonous angiosperms. Three of these metacapnodiaceous species occur outside of New Zealand as well: *Capnocybe fraserae* on an undetermined host in Hawaii and on *Escallonia, Myrceugenia* and *Drimys* in the Juan Fernandez Is.; *Ophiocapnocoma phloiophila* in south-eastern Australia, Hawaii and California; and *Capnobotrys dingleyae* on *Taxus* in Scotland. In North America, *O. phloiophila* and a *Metacapnodium* species grow on montane, mainly ericaceous plants associated with the Cupressaceae that host *Capnocybe spongiosa*. This species also occurs on *Erica, Juniperus* and *Pinus* in Portugal, Spain and Corsica. Of the remaining species of *Metacapnodium*, one has been found on a dicotyledonous host in Sarawak, and the other occurs on *Juniperus* in Scotland.

Capnobotrys neesii is associated with Pinaceae (especially *Abies*), *Buxus*, *Corylus*, *Rubus*, *Sambucus* and *Viburnum* throughout Europe, and in New Brunswick, Canada.

Lastly, among undescribed collections of sooty moulds in Herb. DAOM are members of Euantennariaceae from eastern Canada, Alaska, Hawaii, Chile, France, Corsica, Rhodes, Cuba and Java, and Metacapnodiaceae from the Canary Is., Turkey, Mauritius and China. A *Capnophialophora* occurs on *Pinus* in Greece, species of *Capnobotrys* have been collected in New Zealand, Borneo (on *Ficus*), Chile and the Juan Fernandez Is., Venezuela and Central America (on *Quercus*), and of *Metacapnodium* in Puerto Rico, Dominican Republic, Costa Rica, Patagonia, Juan Fernandez Is., Hawaii, New Zealand, New South Wales, Tasmania and Morocco. The *Metacapnodium* species in Hawaii on recently introduced mango, guava and *Eucalyptus*, and in Morocco, also on *Eucalyptus*, would appear to be themselves recent introductions to these areas. A species of *Metacapnodium* has been found on a montane ericaceous host in the Kivu Province of the Congo.

The geographical distribution of the two families overlaps almost completely, with New Zealand conspicuous as the centre of their spectacular diversification. Considering the amphi-Pacific pattern of distribution alone, New Zealand would also appear to be the centre of their origin; and some long-range means of dispersal might account for the spread of some of the species to south-east Australia and Tasmania, Juan Fernandez Is., and south-western South America, Hawaii and south-western North America. Thus, the sooty moulds might be taken to be of late Cretaceous or even more recent origin, i.e., since the isolation of New Zealand about 80 m.y.B.P. And with that, their sympatric distribution south of the Tropic of Cancer might be explained by long-range dispersal following that of insects and honeydew rather than specific host plants. But other considerations cast doubt on so recent an origin of sooty moulds.

Most sooty-mould species in the northern hemisphere are clearly vicariant, and vicariance argues for a greater antiquity of the two families (Cracraft 1975). Furthermore, honey-dew-producing coccids are probably less capable of long-range dispersal than their host plants; and this incapacity, coupled with the low probability that two families of specialized fungi could achieve a disjunct yet tightly overlapping pattern of distribution through random dispersal, leads us to visualize sooty-mould distribution as more probably overland with migrating biotas, before 80 m.y.B.P. The prevalence of sooty moulds in New Zealand might still reflect their centre of origin there, but could also indicate relic mycota in an area blessed with a long and uninterrupted period of equable oceanic climate. The greater antiquity and overland migration makes more understandable the occurrence, especially of the Metacapnodiaceae, on many archaic angiosperms in the southern hemisphere and endomycorrhizal conifers in North America, the existence of a relic group of vicariant species in tropical South and Central America, and the frequent association of sooty moulds with *Nothofagus* both in South America and New Zealand.

If both sooty-mould families go back in time as far as the early Cretaceous, the absence of endemic species in Africa may have a climatic rather than geological basis. Prior to 90 m.y. B.P. and Africa's separation from South America, the supercontinent had a semi-arid climate. Later, during the Neogene, a prevailing dry climate resulted in a marked impoverishment of the angiosperm flora (Raven & Axelrod 1974). Today, climatic conditions that might favour sooty moulds, adapted as they are to cool oceanic climates, exist only on isolated points of higher

elevation that are the result of a post-Miocene upthrust or volcanic activity. On the other hand, Cretaceous Laurasia, fragmented by epicontinental seas, may have provided suitable niches for oceanic sooty-moulds, inasmuch as the flora of late Cretaceous southern Alberta, for example, was much like that of present-day lands of the south-west Pacific (D.M. Jarzen pers. comm.). The subsequent cooling and widespread drying of the Laurasian climate, followed by glaciation, appear to have reduced the range of sooty moulds to isolated pockets of relic oceanic climate, and to have favoured the evolution of species adapted to a mediterranean climate. The present disjunct distribution of these fungi, especially of *Capnocybe spongiosa*, parallels that of mediterranean sclerophytic vegetation whose once continuous range became fragmented by the orogenic events of the late Pliocene and Quaternary (Axelrod 1975).

RELIC GROUPS OF ASCOMYCETES: THEIR TELEOMORPHS AND ANAMORPHS

The fungi with which we have concerned ourselves here represent the tips of divergent and convergent lines of evolution, and attempts to derive -- from them -- other climax groups of present-day Ascomycota are doomed to fail. Nevertheless, they are significant because of the long history that is reflected in their hosts and geographic distribution, and the conservatism that was imposed on them by their geographic isolation or association with relic groups of plants in areas of relic ecology or climate. Singly or in combination, such circumstances would favour the survival of archaic adaptations. And an interpretation of these archaic characteristics, within the framework of chronology deduced in the preceding paragraphs, may permit a reconstruction of the ancestral types and the direction of evolution in the Ascomycetes.

To recapitulate the chronological sequence we may consider plausible for the Coryneliaceae, they appear to date back at least to the early Cretaceous (120-135 m.y.B.P.), or may be of even considerably earlier, Gondwanalandian if not Pangean, origin at the start of the Jurassic, 180-200 m.y.B.P. Their specific association with *Podocarpus*, especially sect. *Eupodocarpus*, with which the parasites survive in mountainous refuges, points to a long period of coevolution, conservatism and stability, the conditions under which we may expect a retention of primitive ancestral features. The mycelium is endophyllous, protected by host tissues and, consequently, undifferentiated. The ascomata, on the other hand, occur on leaf surfaces and are widely exposed, an existence to which they are crudely adapted by the thickness and strong melanization of walls, which account for their massive size. The ascomata are either astomous or they open by a cleft or simple pore. Being loculate by lysis, they are dothideaceous by definition, but their asci are not bitunicate. Thin-walled, long-stalked and deliquescent, lacking apical apparatus and therefore not typically unitunicate, the asci are not accompanied by interascal tissue of any kind. This kind of centrum and especially of ascus, appears to be of the archaic type that might have characterized an early Mesozoic, Pangaean ancestor of both the bitunicate and unitunicate lineages. The ascospores are liberated into the locule, from which they are extruded in hygrophilic mucilage. The lack of sophisticated mechanisms for ascospore release and active discharge reflects a primary dependence on water for dispersal, though in modern Coryneliaceae it is probably achieved by arthropods. The use of arthropods as vectors may have developed early, providing an increased range of dispersal. Meanwhile, the lysigenous action that initiates the formation of ascigerous locules may also

have prepared the fungus for the initiation of an anamorphic phase. From the partly lysed cells lining the locular cavity, a regeneration (of which most fungus cells are capable under certain conditions) could have resulted in the formation of simple anamorphic propagules. With the establishment of dikaryotization, the functioning of the simple anamorphic diaspore as a spermatium might have been a facultative ability, becoming fixed through the selective pressure of wide-ranging dispersal, as postulated by Savile (1976) for the evolution of pycniospores in the rusts. Increasing the opportunity for heterokaryotization, the spermatial morph would become separated from the teleomorph in time, and then in space, in separate locules, as in some species of *Corynelia* (Fitzpatrick 1942) and *Caliciopsis pinea* (Ray 1936).

The role of arthropods in directing the evolution of fungi such as rusts and Coryneliaceae, through a progression from acting as predators to assuming the role of agents of dispersal and eventually of spermatization, is only one example of the many complex relationships between the two groups of organisms. Honeydew as a source of carbohydrate may have been utilized by Ascomycetes since the Mesozoic. Of the honeydew-producing insects, aphids and scyllids have a fossil record dating back to the Permian, and coccids (scale insects) may represent an even earlier group (W.R. Richards pers. comm.). According to Downes (1972, and pers. comm.), the availability of sugary exudates led to the diversification of holometabolan insects long before the evolution of foliar and floral nectar in plants initiated the dramatically consequential interdependence that now exists between plants and pollinating insects. If the availability of honeydew made such a profound impression on the direction of the evolution of insects, it seems inconceivable that highly opportunistic Ascomycetes would have failed to adapt to this nutritional treasure and be similarly affected. Today, the classic utilizers of honeydew among fungi are the sooty moulds. Yet none of the modern representatives qualifies for a place among the more archaic groups of Ascomycetes.

The typically ascolocular centrum-organization of the Euantennariaceae and Metacapnodiaceae makes it difficult to visualize an origin coinciding with the appearance or early history of honeydew insects or even the Coryneliaceae. Our interpretation of the present-day pattern of the relic distribution of the sooty moulds under consideration calls for the fragmentation of a widespread sooty-mould mycota in the first half of the Cretaceous. Admittedly, this pattern is not clear-cut, because it appears to be the result of climate rather than tectonic developments. Furthermore, we have not considered the insects with which these fungi have coevolved; and thereby we have disregarded data that may prove significant. In the Euantennariaceae and the Metacapnodiaceae, two lines of Loculoascomycetes reached a high degree of morphological similarity through a long period of parallel evolution. Modern sooty moulds offer no clues to their ancestry -- neither which of the two families descended more directly from the ancestral sooty mould, nor what the appearance of that ancestor may have been. If ancestral sooty moulds appeared before the major groups of bitunicates diverged, we can expect that stock to be long extinct.

Nevertheless, we may be able to glimpse something of the structure of an early Loculoascomycete by examining the Parmulariaceae, which we traced to the southern hemisphere of 90-135 m.y.B.P., that is, to the time of the first appearance of angiosperms in the fossil record. Although the origin of the Parmulariaceae may have preceded that of the angiosperms, their diversification coincided with and paralleled that of their angiosperm hosts. This concurrence is seen in the taxonomically and edaphically vicariant taxa occurring on angiosperms,

in contrast to the pteridicolous species which remain little changed on their primary hosts in areas of relic environment. The success of the Parmulariaceae in adapting to a wide range of angiospermous hosts, and their present-day relic distribution on lower vascular plants, do not speak of a long period of co-evolution with ferns and austral gymnosperms, but rather point to youth and genetic vigour at the time of the appearance of the angiosperms.

The ascomata of the Parmulariaceae are superficial or subcuticular, scutelliform, arising from a more or less well developed endophyllous hypostroma, and are usually constructed of vertical or horizontal radiating files of strongly melanized cells, and open by means of hysteriform splitting. Their asci are relatively undifferentiated, bitunicate but not of the 'jack-in-the-box' type, and accompanied by pseudoparaphyses. The anamorphs known in species of *Palawania*, *Rhagadolobium* and *Inocyclus* are peltasteraceous *Palawaniopsis*, *Queenslandia* and *Naothyrsium*. These anamorphs are clearly derived from stromatic locules that have achieved spatial independence from the teleomorph, though the two forms still remain organically or ecologically associated. The conidia arise from simple conidiogenous cells, which normally line the roof of the pycnidium. They are unicellular, delicate, sometimes resembling what are spermatia in other groups, and quite possibly functioning as dikaryotizers as well as, if not rather than, propagules.

The last group under consideration is the Phacidiales. These are clearly a Laurasian group. If we may, as we do, judge by the disjunct distribution of the species occurring on more ancient endomycorrhizal conifers (*Ceratophacidium* on *Sequoia* in western North America, and *Bifusella* on *Cunninghamia* in Okinawa), although their ancestors may have been present in the early Cretaceous, adaptive radiation seems to have been delayed. It appears to have taken place only in the late Cretaceous or even in the Tertiary, possibly only after the cooling of the climate in the temperate zone of the northern hemisphere, and following the mid-Cretaceous disruption of the direct dispersal route to South America, and the establishment of the tropical climatic barrier later in the Tertiary, which largely prevented the spread of these fungi into the southern hemisphere.

The ascoma of the Phacidiales is more or less immersed in host tissue, externally blackened by melanization, and opening by the rupturing of this covering to expose solitary or multiple hymenial locules. The stroma is often composed of vertically oriented files of cells as in many dothideaceous Loculoascomycetes. The asci are cylindrical (long-stalked in *Hypoderma*), accompanied by paraphyses, and discharge their ascospores forcibly by the unplugging of a simple pore in the thickened apex. The ascospores are colourless, delicate, often enveloped by mucilage. The anamorphs, *Phacidiopycnis* and *Discula* in the Phacidiaceae, *Periperidium*, *Ceuthospora* and *Myxofusicoccum* in the Cryptomycetaceae, and *Leptostroma*, *Labrella*, *Hypodermina*, *Melasmia*, *Colpomella*, etc. in the Rhytismataceae, are phialidic, bacillar, morphologically and probably functionally spermatial as well as propagative, borne in locules within the ascomata, or in separate loculate pycnidial conidiomata. A trend toward the reduction of stromatic tissue, especially of the highly melanized roof tissues, results in sporodochial conidiomata.

AFFINITIES WITH MODERN ASCOMYCETES

Coryneliaceae: The passive release of ascospores characteristic of the Coryneliaceae is also a conspicuous feature of the Coronophorales, Halosphaeriaceae, Melanosporaceae and the Ophiostomataceae. However, only in the Coryneliaceae and the Coronophorales can this feature be

considered archaic, reflecting a primary lack of adaptation of both the ascus and the ascoma. The Coronophorales, a distinctive group of broad-spectrum saprobes on woody substrates, merit special attention in future speculations on the phylogeny of the Ascomycetes. The Halosphaeriaceae, Melanosporaceae and Ophiostomataceae are highly specialized -- morphologically, physiologically and ecologically -- a specialization inconsistent with their lack of a forcible discharge mechanism unless this loss indicates a reversal to an archaic condition imposed by a specialized environment. The loss of such a mechanism by the Halosphaeriaceae, for example, is clearly the result of their adoption of an aquatic habit; they still betray a former specialization in the presence of an ostiole and the cylindrical shape of their deliquescing asci (D.W. Malloch pers. comm.).

The status of the Melanosporaceae and the Ophiostomataceae is more open to discussion (see this volume, Chap. 13). The asci in the Melanosporaceae and some Ophiostomataceae (e.g., some species of *Ceratocystis*) are 'corynelioid'; but this does not detract from the validity of the arguments presented by Redhead & Malloch (1977) in support of a derived position for the Ophiostomataceae. This family's association with northern hemisphere trees, especially conifers, as saprobes or parasites or, indirectly, through symbiosis with ambrosia beetles, does not suggest a pre-Cretaceous origin, but rather points to a secondary adaptation for dispersal by insects.

Parmulariaceae: The morphological similarity between the Parmulariaceae and Asterinaceae, which appears to go beyond that imposed by the sharing of an ecological niche, makes it possible to visualize a direction for the evolution of the Asterinaceae from an immediate common ancestor of both families. The direction has been toward a separation of locules, a reduction of adjacent stromata to the form of scutelliform thyriothecia usually one layer of cells deep, a spreading out of interlocular stromatic tissue into a highly melanized superficial mycelium, and a replacement of the absorptive hypostroma by intraepidermal haustoria. These adaptations to a foliicolous existence through a streamlining of the thallus were made possible by the melanization of vegetative and propagating organs, and must account for the successful diversification and extension of the Asterinaceae accompanying the expanding availability of angiosperm leaves since the Cretaceous.

Parallel evolution seems to have taken place in the microthyriaceous and micropeltaceous bitunicates, some of which achieved a climax of simplification by the elimination of both the external interlocular, and the internal absorptive, mycelia. The pattern is also repeated to some extent in the Meliolaceae and the Parodiopsidaceae, whose thick-walled but poorly differentiated asci point to a considerable antiquity in the retention of this ancestral form. Fitzpatrick (1920, 1942) saw phyletic connections between the Parodiopsidaceae and the Corynelîaceae; *Meliolina* has strong ties with Gondwanalandian hosts in the southern hemisphere (Pirozynski 1974).

Phacidiales: According to Holm & Holm (1977), the Phacidiales are related to the Leptopeltidaceae, a family occurring in the northern hemisphere, mostly as saprobes on fern petioles. The ascomata are scutelliform, composed of radial files of cells, and split open by hysteriform or irregular slits. The asci are borderline in form, between bitunicate and unitunicate in organization. Because of their thick walls, they have been traditionally regarded as bitunicate, a view which is reiterated elsewhere in this volume. However, according to Holm &

Holm, the ascus is unitunicate, with a rudimentary apical apparatus in the form of an I-negative annular 'collar' which projects downward within the apical thickening. Leptopeltidaceous anamorphs are locular pycnidial conidiomata that resemble the ascomata in the family, and belong to the form-genera *Leptothyrium* and *Pycnothyrium*. These several features of the Leptopeltidaceae are shared not only by the Phacidiales by also by the Parmulariaceae.

EVOLUTION OF PLEOMORPHISM

The evolution of an anamorphic phase in Ascomycetes was undoubtedly in response to the advantage of having accessory propagules that could build up the population during favourable growing conditions. The production of such propagules necessitated at least a partial emergence from host tissues by the generative thallus, and the elaboration of propagules coping with the hazards of desiccation and radiation inherent in aerial dispersal. If our picture of ancestral forms is accurate, the exposed parts of these early fungi were already melanized, and therefore resistant propagules could be developed through the modification of components pre-adapted to the task by melanization. Indeed, this ability of Ascomycetes (and apparently also of the rust fungi, see Savile 1976) to exploit the protective potential of melanins accounts for their initial success on land.

Pleomorphic evolution in Ascomycetes followed two separate lines, both of which are seen in the relic groups discussed above. The first approach is seen in the Coryneliaceae, in which anamorphic locules arise within the protective confines of an exposed, melanized ascostroma. The propagules (or perhaps spermatia) are simple unicells, delicate and ephemeral, with only a mucilaginous envelope offering short-term protection, primarily against desiccation. Here, defense is largely provided by the fructification's superstructure, and the fugacity of the propagules is partly offset by their numbers. The same pattern is continued in the Parmulariaceae and the Phacidiales, though both groups have advanced toward the achievement of a more complete separation of the anamorph from the teleomorph in space and time.

The second stratagem is well demonstrated by the sooty moulds, especially the Metacapnodiaceae. In order to use honeydew or plant exudate, the fungus as a whole -- the entire thallus, somatic as well as reproductive -- had to emerge onto exposed surfaces that were sprayed from above by hypophyllous coccids (cf. Downes 1974). This exposure was made endurable by the melanization of the entire thallus, hyphae as well as fruit bodies. Successful colonization of external substrates called for the mobilization of all protective devices available, as is seen not only in the degree of melanization achieved -- rarely matched in nature by other organisms -- but also the evolution, in some groups of sooty moulds, of double-walled hyphae and supplementary gelatinous sheaths. Once the emergence of mycelium had been achieved, and the development of the ascoma from a cell of that mycelium, the road was open for the elaboration of mycelial dematiaceous anamorphs. Simple fragmentation of superficial hyphae led to progressive elaboration of mechanisms that produce a plurality of conidia at the lowest possible cost in terms of the destruction of the conidiogenous thallus. Almost totally avoided were mechanisms requiring exposure of the protoplasts as in a phialide.

This evolutionary sequence can still be seen in the metacapnodiaceous and euantennariaceous sooty moulds occupying the lands bordering the south Pacific, especially New Zealand. Because of the geographic isolation and climatic stability that have made New Zealand a biological

archive, the evolution of anamorphs in sooty moulds did not call for the destruction of their prototypes. In *Ophiocapnocoma*, the hyphae still fragment by simple disarticulation across a septum. In *Antennatula* and *Capnokyma*, some branches of repent hyphae or erect, setiform hyphae secede to serve as phragmoconidia. Their secession is not haphazard but takes place at a predetermined spot, marked by a constriction at the junction with the conidiophore. An elaboration of this mechanism, designed to produce a plurality of conidia, occurs in the *Antennatula* anamorph of *Euantennaria mucronata* (Hughes 1974). In this species, percurrent proliferation of the conidiophore results in the development of an annellide. Delayed secession of a terminal conidium may lead to subapical proliferation of a conidiogenous cell and sympodial sequence of conidiogenesis as shown by *Capnocybe*. At the same time, heavy melanization, which would prevent the proliferation of a hypha (or a portion of it) from a broad area but permit localized growth through replasticization or dissolution of a minute spot, may have led to establishment of the tretic ontogeny demonstrated by the *Hormiokrypsis* anamorph of *Ophiocapnocoma*. The strength of the resulting propagules is not in numbers but in resistance and longevity.

Locular anamorphs, as seen in the relic Coryneliaceae, Parmulariaceae, Leptopeltidaceae and Phacidiales, occur in most of the modern groups of Ascomycetes, both bitunicate and unitunicate. The locular anamorph, therefore, appears to be as old as the Ascomycetes themselves, and may have even been inherited by the Ascomycetes from their ancestors, whatever they were. The main departure from this pattern has been the elaboration of the 'mycelial' anamorphs seen in the metacapnodiaceous and euantennariaceous sooty moulds. However, many other modifications of, and departures from, the two models are registered in modern Ascomycetes, both bitunicate and unitunicate. The origins of most of these later adaptations are lost in their complexity.

The bitunicates: In the Asterinaceae, which successfully colonize leaf surfaces, the locular anamorph has departed only slightly from the generalized type of the Parmulariaceae by the melanization of conidia. But evolution of mycelial anamorphs has been achieved in the Asterinaceae -- in *Asterodothis (=Eupelte)*, *Clypeolella* and others. Mycelial anamorphs also occur in convergent and parallel families: the Englerulaceae, the Parodiellinaceae, and some of those sooty moulds that have retained locular anamorphs. Abstriction of conidiiform branches from setiform hyphae takes place in *Acrogenotheca*. In *Brooksia*, a series of conidiiform branches arises from an annellide. The *Helicosporium* anamorph of *Tubeufia* may merely represent a sympodial ontogenetic variant.

Another kind of mycelial anamorph that usually supplements pycnidia or spermatia may have its beginning in the accidental damage suffered by exposed hyphae or their various adaptive modifications. A simple regenerative mechanism in the *Septoidium* anamorph of the Parodiellinaceae involves percurrent proliferation through a spent conidiogenous cell. A more streamlined annellidic version of percurrent regeneration may be demonstrated by *Stigmina*, which produces conidia from cells of juvenile ascostromata of *Otthia*. The production of a succession of conidia from sympodially proliferating, superficial, hypha-like conidiophores is frequently seen in the Mycosphaerellaceae. The anamorphs *Cercospora* or *Ramularia* have departed little morphologically from tufts of hyphae that may emerge from substomatal ascoma-initials, sometimes in response to excessive moisture. Indeed, if the transformation of hyphal tufts into conidiophores of *Cercospora* or *Ramularia* could be as easily achieved as the regression of these conidiogenous hyphae into hyphal tufts, much might be learned about the relationships of these

fungi. The primary function of setae is protection and, in performing this function, the setae are themselves exposed to damage. A regenerating seta often reproduces, at its broken apex, the mycelial anamorph characteristic for the species. Selection for setae of potential double value, or the evolution of setiform conidiophores, might account for several examples of anamorphs in the bitunicates. Mycelial setae may be identified in the *Periconiella* anamorph of *Allosoma*, and ascomatal setae in the *Eriomycopsis* anamorph of *Melioliphila*. In the closely related *Chionomyces*, percurrent regenerative proliferation and sympodial conidiation occur side-by-side on the same conidiophore.

There is a rare occurrence of phialidic mycelial anamorphs in bitunicates and groups characterized by undifferentiated asci that are at least initially thick-walled, such as are found in Parodiellinaceae, Meliolaceae and some tropical hyperparasites which we tentatively assign to Hyalodermataceae (cf. Pirozynski 1977). The rare occurrence of these mycelial phialides in these groups may perhaps be explained by their early evolution in the southern hemisphere. Unlike Laurasia (where climate was moderated by epicontinental seas), Gondwanaland and, later, the supercontinent of West Gondwanaland of the second half of the Mesozoic, may have been largely hot and arid. This climate would explain not only the widespread melanization of bitunicates but also the suppression of 'open-ended' mycelial phialidic anamorphs. In a corollary to this trend, the liberation of phialides from protective pycnidia would have been largely prevented -- a strategem that appears to be very different from that adopted by the unitunicates.

The unitunicates: The first indication of the opening of anamorphic locules appears in the Phacidiales, where a gradual reduction of the stromatic covering and its eventual elimination leaves naked cushions of densely packed phialides within the outer tissues of the host. The next step leads to acervular anamorphs: annellidic in the *Seimatosporium* and *Pestalotia* anamorphs of *Discostroma* and *Broomella*, phialidic in the *Colletotrichum* anamorph of *Glomerella* et al.

Then follows the complete emergence of sporodochial and hyphomycetous, mainly phialidic, anamorphs in many Helotiales and most Hypocreales. It may be significant that, in these two orders, the liberation of the anamorph from the constraint of a pycnidium is accompanied by liberation of the thallus from the constraint of effective but probably unwieldy melanins, and their replacement by cytoplasmic pigments.

It seems that, in the unitunicates generally, melanization is less pronounced than in the bitunicates and, where retained, may have remained in response to selective pressures other than those imposed by climatic conditions. Some of the unitunicates with most strongly melanized propagules are adapted to animal dispersal by ingestion, in which case melanins would provide protection against digestive juices and other hazards of the internal environment of an alimentary system.

As in the bitunicates, the origin of some of the anamorphs in the unitunicates can be traced to various kinds of superficial mycelium: hyphae accompanying ascomata as in the *Oedemium* anamorph of *Chaetosphaerella*, or borne on ectostromata as in many Xylariaceae, the mycelial setae of *Catenularia*, *Codinaea*, and *Zanclospora* of *Chaetosphaeria*, or *Chaetochalara* of *Calycellina*, and the ascomatal hairs or setae of *Dicyma* in *Ascotricha*.

However, neither in the unitunicates nor in the bitunicates do these adaptations account

for the full spectrum of anamorphic expression. The obvious advantage of producing a population-building 'summer' propagule would exist wherever less than equable climates occurred, leading to selection for anamorphic devices of many kinds, among them the apparently separate elaboration of tretic morphs from superficial or immersed mycelium in the Pleosporaceae, and hyphomycetous morphs in the unitunicates. The cooling and drying of climate in the northern hemisphere, in the second half of the Tertiary, might have favoured a shift to self-fertility and the re-adaptation of spermatia to a propagative function; and a more pronounced differentiation of seasonality, the evolution of a dedicuous habit in the host, and a slower rate of litter decomposition, would favour saprobism in the fungus, with an alternation of anamorphic and teleomorphic phases, separated in time and space, achieving a trophic 'heteroecism' that made the most of whatever was available as a source of nutrient and a means of survival.

The complexity of these evolutionary patterns is further compounded by migration of both bitunicates and unitunicates into each other's domain with new, more adventurous hosts such as grasses, and the availability of broad-ranging dispersal agents from herbivores to man himself. Climatic and biotic changes since the late Cretaceous should have affected the mycota of New Zealand to a lesser extent that that in other areas. We might, therefore, expect the Ascomycetes of New Zealand to be directly descended from groups that were present there 80 m.y.B.P. Unfortunately, man has been exceptionally active in swamping indigenous biota by introducing exotic plants and animals and -- inadvertently -- fungi. Dingley's (1969) list of parasitic fungi of New Zealand demonstrates this clearly. Nevertheless, even in an inventory strongly biased toward economic and therefore imported plants, with their own parasitic and saprobic fungi, a glimpse of the original situation can be revealed by focusing on indigenous biota. There have been, for instance, surprisingly few 'jumps' of fungus parasites from imported to indigenous hosts, many of which appear to have retained their original mycota. This mycota is represented mainly by 'phycomycetes' and wood-rotting and parasitic Basidiomycetes. The Ascomycetes are few. On ferns, they are represented by sooty moulds and Parmulariaceae. Those on austral gymnosperms stand in contrast to the parasites of imported members of the Cupressaceae and the Pinaceae: sooty moulds and Coryneliaceae versus an assortment of forms typically associated with northern hemisphere forests. The same is true of *Nothofagus*, which hosts sooty moulds, *Cyttaria* and *Trabutia*, while the imported ectomycorrhizal relatives of *Nothofagus*, such as *Castanea* and *Quercus*, host *Nectria*, *Rosellinia*, and *Microsphaera*. The Ascomycetes most conspicuous on, and often confined to, indigenous members of the Cunoniaceae, Epacridaceae, Myrtaceae, Proteaceae and Winteraceae are representatives of groups with undifferentiated asci such as *Meliolina*, *Meliola*, *Irenopsis*, or bitunicate sooty moulds (*Trichopeltheca asiatica* occurs on ninety host plants of which only one is exotic), *Trabutia*, *Vestegrenia* and *Microthyriella*. *Taphrina* has not been reported from any of the native plants of New Zealand.

In summary, all aspects of the biogeography of the Coryneliaceae that we have examined point to the antiquity of this evolutionary line. Its early offshoots still survive as Parmulariaceae whose origin can be traced to Gondwanaland and, apparently, as Leptopeltidaceae in the northern hemisphere. We therefore conclude that Ascomycetes characterized by a dothideaceous centrum and morphologically undifferentiated but functionally bitunicate asci were widespread at the Jurassic/Cretaceous boundary, when several land-bridges or island-chain 'filters' linked Laurasia with Gondwanaland. Since the early Cretaceous, however, the bitunicate line, of which

the Parmulariaceae are surviving early descendants, evolved, dispersed and vicariated in fragmenting Gondwanaland. Simultaneously or more probably later, since mid-Cretaceous and after the disruption of direct links between northern and southern continents, the evolution of unitunicates -- of which the Phacidiales are a conservative early offshoot -- took place in Laurasia. This conspicuous dichotomy in the evolution of the Ascomycetes -- into bitunicates and unitunicates -- thus appears to be the result of separate evolution on different continents and in relative isolation until the latter half of the Tertiary, during which time the first of a series of connections were re-established. The resultant mixing may have been one of the factors behind the diversification of both groups, but not necessarily the chief or only factor. Members of both, at different times and at different stages in their evolution, formed symbiotic associations with algae and elaborated the consortia we call lichens. In some obligate relationships, an independent dispersal of the fungal component could become wasteful, and the adaptation of asci for forcible discharge of ascospores redundant. The evolution of the fungus *qua* fungus, and especially its asci, might then be arrested or even regress. Subsequent de-lichenization (stages of this phenomenon are found in modern mycota) would result in anomalous groups of Ascomycetes, of which the Ostropales (Sherwood 1977, and pers. comm.) and *Massaria* and some of its allies (von Arx Chap. 13) may be examples.

While conceding that lichenized Ascomycetes may contribute substantially to our unravelling of Ascomycotan phylogeny (cf. Cain 1972), and basing much of our own speculations on the present-day biogeography, we must remind ourselves and our readers that we may not ignore the fossil record, however fragmentary. Only in the fossil record can we find less equivocal evidence of ancestral linking groups, most of which, because of their rapid evolution, have failed to survive to the present.

FOSSIL RECORD

The earliest fossil record of a presumed Ascomycete is of Carboniferous 'spores' recovered from coal by maceration, and classified in a fossil morphographic category labelled Sporonites (Horst 1955, Dybova & Jachowicz 1957). Subsequently, similar 'spores' were recorded, also from Carboniferous strata, but under *Chaetosphaerites* Felix (Butterworth & Williams 1958, Staplin 1960, N.F. Hughes & Playford 1961, Playford 1962). Felix (1894) had established *Chaetosphaerites* for an Eocene spore resembling an ascospore of modern *Chaetosphaeria* (cf. *Ch. innumera*) or *Passeriniella* (cf. *P. dichroa*) -- a 3-septate spore with two central cells pigmented and the smaller end-cells hyaline. What the palynologists illustrated under *Ch. polleenisimilis* bears only a most superficial resemblance to the spore described by Felix. As the epithet indicates, the Carboniferous 'spore' resembles a pollen grain, and Horst (1955) may have correctly indicated its affiliation with some extinct group of conifers or pre-conifers. Yet, not all of the 'spores' assigned to this species are of the same kind, and it may be that the simple and branched bodies described under this name by Staplin (1960) and, especially, by Playford (1962) are fungal, though they are clearly not ascospores. Such groups of cells of irregular outline, and with septa perforated by distinct pores, could be taken for early representatives of the Ascomycota, though it is impossible to be sure that they are even fungal. They could be algal. Other Carboniferous microfossils which are claimed to be Ascomycetes and to represent not only hyphae, stromata and sclerotia but also asci and various kinds of propagule, including conidia (Benes 1959), constitute the 'sclerotinites' encountered in pol-

ished thin sections of coal. There is some controversy regarding the identity of sclerotinites. Those who classify them in form-categories labelled Sclerotites, Discoascina, Stellasclerotes, etc., consider them to be petrified remains of fungi on evidence that would not, however, convince most mycologists.

Further evidence of a Palaeozoic fungus of presumed ascomycotan affinity dates back to the terminal Permian, some 240 m.y.B.P. The fossil was found in coastal marine shale of present-day Oklahoma, and described in a new form-category Reduviasporonites Wilson (1962). The abundant fragments, which are accompanied by spores of contemporary vascular plants, are in the form of short chains of moniliform, more or less globose cells about 20 µm in diameter, with coarsely perforate and characteristically collapsed septa. These chains somewhat resemble the mycelium of modern sooty moulds, especially of *Ophiocapnocoma* of the Metacapnodiaceae (cf. Hughes 1967). But although it is tempting to take the fossil fragments as evidence of the antiquity and once wide distribution of ancestral sooty moulds, again the possibility of the algal character of the fossil cannot be ruled out.

The evidence from the earlier periods of the Mesozoic is also very scarce and inconclusive. In a new 'genus' Microsporonites, Jain (1968) illustrated a single species from the Triassic of Argentina. The 'spore' is in the form of a rosette-like cluster of short toruloid chains of cells 8-14 µm in diameter. Their wall is smooth and about a micron thick. No further details were given, and no additional data appear in the illustration, making it difficult to identify the fossil even as a fungus. Also in Argentina, Volkheimer (1969) observed that spores judged to be fungal (presumably ascomycotan) were more numerous in some samples than all other spores and pollen of plants. None of the 'fungus spores', however, was described or illustrated, and our efforts to obtain samples providing satisfactory evidence of the presence of fungi have met with no success. It is, therefore, not until the Cretaceous that unequivocal evidence of the Ascomycota appears in literature on the fossil record. This evidence was first provided by Singh (1971) who recovered, from the Albian (ca. 122-110 m.y.B.P.) of Alberta, a microthyriaceous thyriothecium, two *Sporidesmium*-like conidia of Pluricellaesporites psillatus, and also a spore labelled Dyadosporites ellipsus, which resembles a teliospore of *Puccinia*.

Even earlier Cretaceous rocks, of the Potomac group of Maryland (Barremian to Aptian, 127-122 m.y.B.P.), have yielded an assortment of fungus-like propagules, a selection of which is here illustrated for the first time (Plates 8.I & 8.II). Figs. 8.1-8.4 are of moniliform filaments that resemble Wilson's (1962) Permian Reduviasporonites catenatus or hyphae of the Metacapnodiaceae, though there is no evidence of the tapering that today characterizes the family. Our previous expression of doubt about the Permian record is reinforced by close examination of the fragments illustrated here in which there appears to be common occurrence of intercalary cell division -- rare in fungi but normal in filamentous ulotrichalean, cladophoran and conjugating algae and in Cyanophyta, especially those which have achieved the development of a truly filamentous habit and pit connections. An analysis of the walls or wall residues may well provide a more dependable clue to their identity.

Of the remaining fossils illustrated here (Figs. 8.5-8.33), there can be much less doubt about their fungal, even ascomycotan, character. Hyphae, sclerotia, and a variety of propagular forms can be readily recognized. Those illustrated in Figs. 8.5-8.12 resemble sooty moulds (cf. Hughes 1970, 1974). Here, toruloid mycelia appear to disarticulate into single

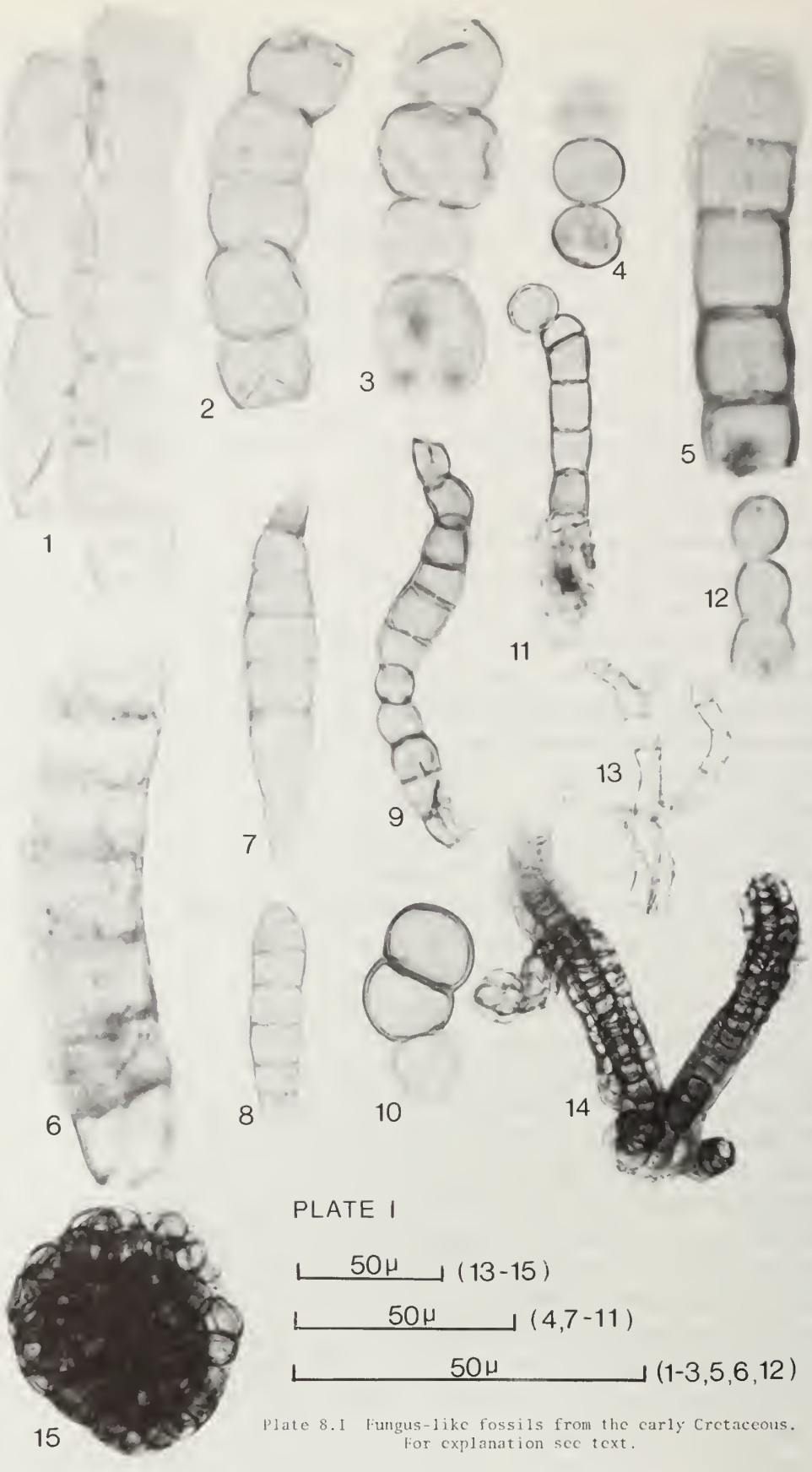


PLATE I

50μ (13-15)

50μ (4,7-11)

50μ (1-3,5,6,12)

Plate 8.I Fungus-like fossils from the early Cretaceous. For explanation see text.

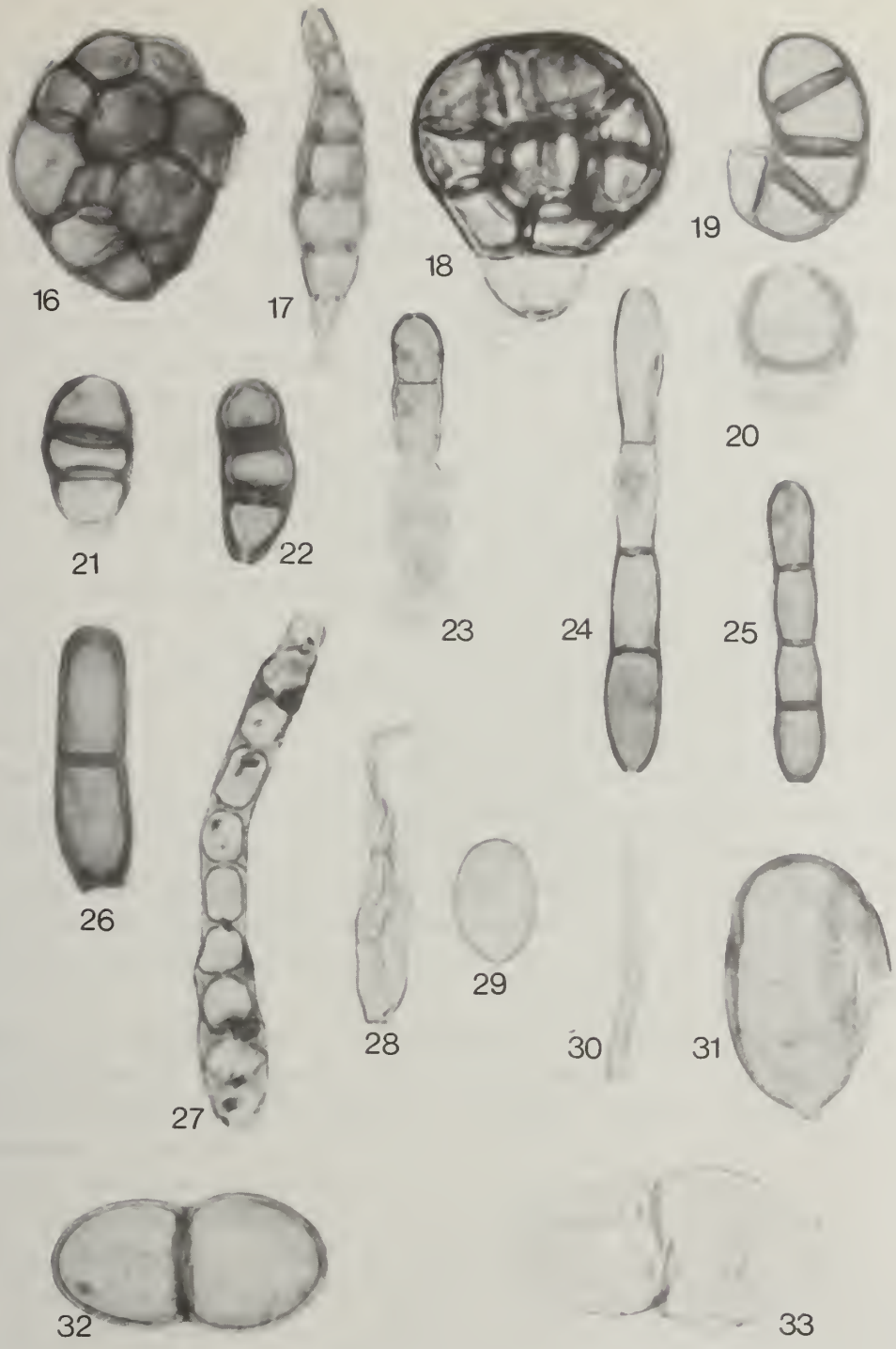


PLATE II

50μ (16)

50μ (17, 23-25, 27, 28, 33)

50μ (18-22, 26, 29-32)

Plate 8.II Fungus-like fossils from the early Cretaceous. For explanation see text.

rounded cells or short chains of cells as in modern representatives. A modification of such thallic ontogeny is shown in Figs. 8.11 and 8.12, where propagating cells are abstricted from hyphae, apparently in basipetal succession. Another variant of thallic development results in the formation of intercalary chlaydospores (Fig. 8.17) much like those of *Xylomyces*. Also represented are terminal chlamydospores resembling those of *Monodictys* (Fig. 8.18), *Cirrenalia* (Fig. 8.19) and *Trichocladium* (Figs. 8.20-8.22). Dispersed catenate conidia of what appears to be either *Heteroconium* or *Corynespora*, or both (Figs. 8.23-8.27), demonstrate tretic ontogeny. Lastly, finely echinulate conidia (Figs. 8.29, 8.31) -- abundant in the assemblage -- show distinct denticulate attachment scars indicative of a sophisticated abstriction mechanism, possible from a sympodially proliferating conidiophore such as Fig. 8.30 can be interpreted to represent. These conidia, of which the vast majority fall within a fairly narrow size range (only their extreme sizes are illustrated), resemble some of the living members of *Ramichloridium*. The two ascospores (Figs. 8.32, 8.33) point to marine genera like *Helicascus*, *Halotthia* or *Pentopeira* which, like *Xylomyces* and *Cirrenalia*, would not be out of place in rocks of the Potomac Group, which are sedimentary units formed in a fluvial-deltaic, marine situation (Wolfe et al. 1975).

This assemblage as a whole is noteworthy as exemplifying the morphological differentiation of asexual propagules, and especially of the diversification of their inferred ontogenetic mechanisms. It demonstrates that, at a time in the early Cretaceous when angiosperms were just emerging from a subordinate role in the terrestrial flora, Ascomycetes already appear to have been both numerous and diversified, especially in their accessory asexual propagules. In other words, pleomorphism was already well and probably long established. Another point of interest in this find is the similarity of the fossil mycelia, conidia, and especially ascospores, to those of bitunicate rather than unitunicate Ascomycetes. The one exception may be the papulaspore-like ball of cells (Figs. 8.15, 8.16) which today might indicate the Melanosporaceae -- though, as yet, without certainty.

During Cretaceous times, when angiosperms showed an almost explosive evolution, Ascomycetes -- according to published accounts -- demonstrated little innovation. Both toruloid and cylindrical, stout, 'capnodiaceous' hyphae, fragments of *Sporidesmium*-like phragmoconidia or *Xylomyces* chlamydospores (Pluricellaesporites), helicoid conidia of *Cirrenalia* (Involutisporonites), denticulate ameroconidia (Lacrimasporonites) and didymosporous ascospores (Dyadosporites) dominate the fossil records of terminal as well as early Cretaceous deposits, as is shown by Clarke (1965) and Srivastava (1968). Clarke's Involutisporonites foraminus appears to be morphologically close to a marine *Cirrenalia* (e.g., *C. tropica*) or *Zalerion* (e.g., *Z. maritima*). Less strongly coiled conidia of *Cirrenalia* (cf. *C. macrocephala* or *C. pseudocephala*), as well as those of another marine Hyphomycete, *Culcitalna*, appear to be of common occurrence in the Upper Cretaceous (Maestrichtian) brackish-marine basins of Alabama (D. Jarzen pers. comm.). It is, then, during the first half of the Tertiary period that the known fossil record bears witness to a proliferation and diversification of ascomycotan propagules, both ascospores and conidia, which are representative of unitunicate as well as bitunicate fungi.

One of the difficulties of the fossil record is that propagules usually occur as separate entities. In their dispersed state, different sexual and asexual propagules, many of them representing the pleomorphic expression of a single organism, are treated as if they were aut-

onomous form taxa. Until life cycles are fully elucidated in recent Ascomycetes, much of the value of fossil fungal *sporae dispersae* for reconstructing the past mycogeography, ecology and phylogeny of fungi will remain unexploitable. Nevertheless, the fact that pleomorphism was widespread by the early Tertiary, and that it probably played the same roles as it does today, is established by the fossil fungi that have been recovered with their substrates. Trichothecia of *Trichothyrites* (cf. *Trichothyrium asterophorum*) are often accompanied by their *Spegazzinites (Isthmospora)* conidia, the foliicolous *Vizella memorabilis* (cf. *V. oleariae*) bears both thyriothecia and pycnidia still containing their respective spores, and the endoxylous *Cryptocolax clarnensis* has, like the modern *Xylogone sphaerospora*, fertile cleistothecia associated with arthroconidia.

We have given you no more than a glance at what may be available in the fossil record of fungi. Some support has been shown for the postulation we made earlier that bitunicate fungi made their mark in Ascomycete history before unitunicates. Not only do we find what appear to be bitunicate members of the Ascomycota present in early Cretaceous Euramerica, but also they already demonstrate specializations of various kinds, including even invasion of and adaptation to marine environments. Nevertheless, our contention that the evolution of bitunicate lines preceded that of unitunicates cannot be considered established as fact, for we are fully aware of the selective process of fossilization itself. The very protective strategy adopted by bitunicates, the melanization of mycelia and propagules as well as of fruit-bodies, would selectively ease their fossilization and recovery. The fossil record is necessarily fragmentary; and what there is in it remains practically unexplored. It is undoubtedly premature to assign much significance to isolated and insufficient samples. But neither may we ignore the evidence that has been found in fossil remains, or deny ourselves their potential value for reconstructing the past history of the fungi.

ACKNOWLEDGMENTS

We extend our sincere thanks to Dr. S.J. Hughes, D.W. Malloch, E. Müller and D.B.O. Savile, for supplying many ideas developed in this paper, to Mr. R.G. Day for compiling graphic presentations of some of the data, and to Dr. J.A. Doyle for supplying slides of fossil fungi illustrated in this paper.

After that biogeographic discussion which ranged so widely in time and space, we come to several chapters that focus on specific groups in which teleomorph-anamorph connections are well known. Close scrutiny may reveal that teleomorph groupings can be heterogeneous or polyphyletic (as in the case of the 'Plectomycetes'), and that the phialide, that pillar of anamorph systematics, may itself have evolved more than once.....

9
Phialidic Hyphomycetes and Their Teleomorphs - an Analysis

C.V. Subramanian

This chapter is dedicated to the memory of Dorothy Fennell, who did so much work on the Aspergilli, and who very kindly placed at my disposal many of the cultures used in our studies.

The relationship of phialidic Hyphomycetes to their teleomorphs can be understood properly only from a precise knowledge of phialidic conidiogenesis, and of as many parameters as possible relating to their teleomorphs. Although we have valuable information on many connections, bibliographic correlations cannot always be relied on, because of the possibility of misdeterminations, or the inadequacy of supporting experimental evidence. I believe, therefore, that existing information is inadequate, and a great deal of further work is needed (Subramanian 1971a). It is with a view to filling this lacuna that we are studying developmental morphology in both teleomorph and anamorph of some taxa whose conidia show phialidic ontogeny. The teleomorphs we are investigating belong either to the Eurotiales or the Hypocreales, as currently classified. The teleomorphs of *Aspergillus* have received special attention (Subramanian 1972c, Malloch & Cain 1972, 1973, Wiley & Simmons 1973, Fennell 1973).

In this paper I propose to summarize the advances we have made in the understanding of phialidic conidiogenesis since Kananaskis-I, and then discuss the relationship of phialidic Hyphomycetes to their teleomorphs, chiefly in the Ascomycotina, with special reference to recent work on the developmental morphology of the Eurotiales.

PHIALIDIC CONIDIOGENESIS -- AN ANALYSIS

At Kananaskis-I our knowledge of the ultrastructure of conidiogenesis was very meagre and was limited to one or two papers. References to a few papers on the phialidic mode which had appeared at that time but to which no reference was made at the Conference were incorporated in my paper (Subramanian 1971b) subsequently, for the sake of completeness. Since then a great deal of work on the ultrastructure of conidiogenesis has appeared, demonstrating that there are variations in the phialidic mode. At least four distinct types can be recognized in which the conidia may be described as follows (terminology from Subramanian 1972b):

1. Synechidic, etunicogenous, exporrectic, pseudocatenate or discrete, slimy, sometimes glomerate, e.g., *Thielaviopsis basicola* (Delvecchio, Corbaz & Turian 1969), *Phialocephala dimorphospora* (Carroll & Carroll 1974).

Hawes & Beckett (1977c) have questioned the validity of my suggestion that conidium formation in *Thielaviopsis basicola* is by protoplasmic cleavage followed by cell wall deposition around the cleaved-out protoplasmic mass (I did not refer to "free-cell formation" at all in my paper as erroneously suggested by these authors). While I concede that further evidence may be need-

ed to support my interpretation, I find nothing in the electron micrographs they provide to contradict my interpretation; if anything, they seem to lend further support to what I said. Their reference to septal pores between adjacent conidia is certainly important, but no electron micrographs are presented to support this statement.

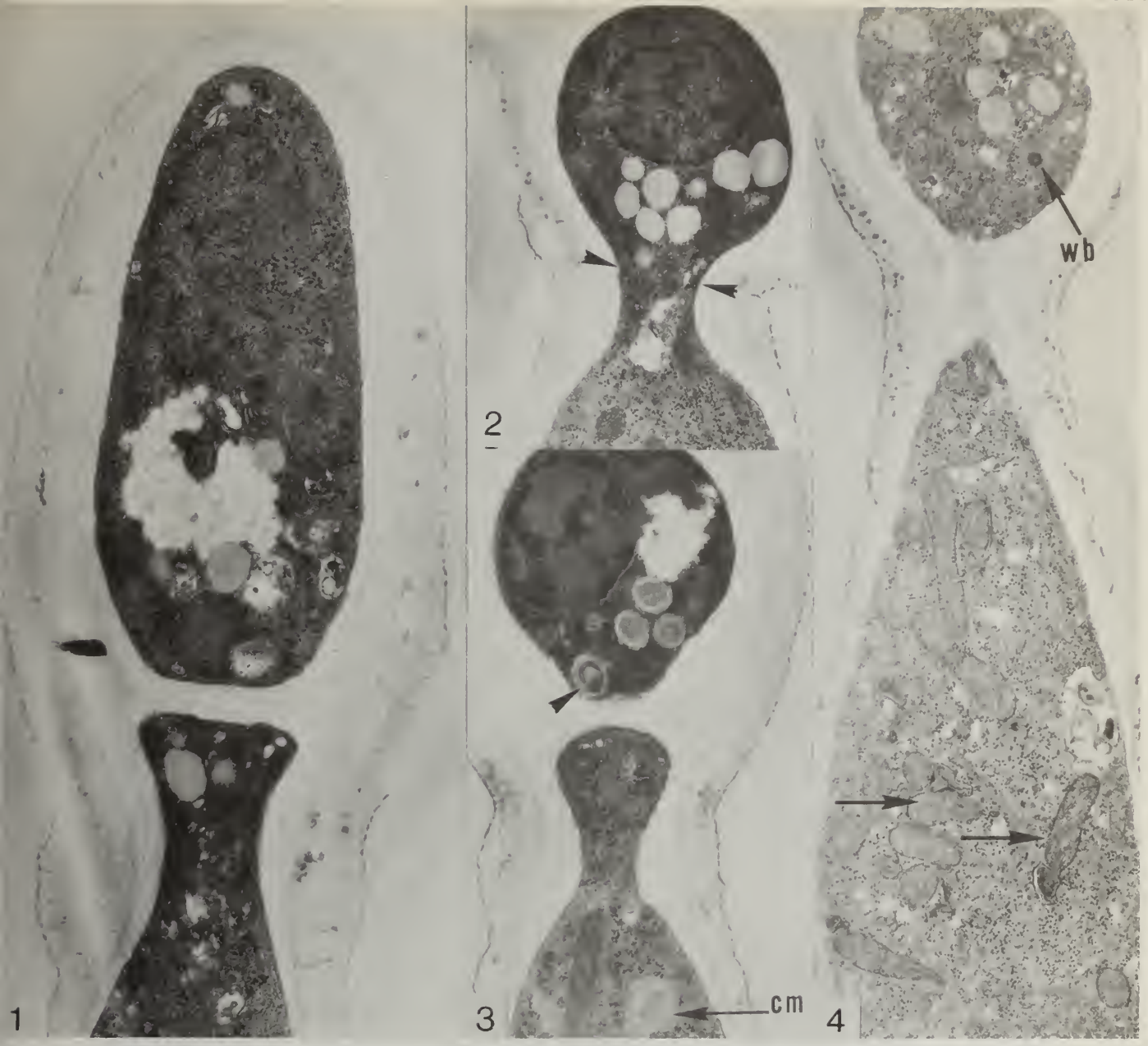
My interpretation of conidiogenesis in *Phialocephala dimorphospora*, as seen from the transmission electron micrographs of Carroll & Carroll (1974), is that the first conidium is formed within the apex of the phialide by cleavage of cytoplasm, followed by wall formation around the cleaved out cytoplasm, rather than by delimitation by septum formation. In the development of subsequent conidia also, a cytoplasmic mass is presumably pinched off from within the phialide each time and then becomes surrounded by a new wall, the whole sequence being repeated. Though they mention septa as delimiting the first and later conidia, Carroll & Carroll state that "the process of septum formation has been only rarely observed ... The mature septum is non-perforate and without associated Woronin bodies; a pore has never been seen at the base of either primary or secondary mature conidia in the hundreds of sections examined" (Carroll & Carroll 1974:2122). My tentative interpretation of these observations is that there is, in fact, no septum development, but only a pinching off or rounding off of cytoplasm within the phialide, followed by deposition of wall material around each cleaved-out cytoplasmic mass (Figs. 9.1-9.4).

2. Synechidic, novi-cum-penititunicogenous, porrectic, catenate, dry, e.g., species of *Penicillium*, *Aspergillus* (see Subramanian 1972b), *Metarrhizium anisopliae* (Zacharuk 1971, Hammill 1972b, Figs. 9.5-9.7), dark conidia of the *Chalara* state of *Ceratocystis adiposa* (Hawes & Beckett 1977b).
3. Pseudosynechidic, tunicogenous (first conidium totitunicogenous, later conidia penititunicogenous, possibly all conidia penititunicogenous), porrectic, percurrent, solitary, glomerate, slimy, sometimes pseudocatenate, e.g., microconidia of *Neurospora crassa* (Lowry, Durkee & Sussman 1967, Oulevey-Matikian & Turian 1968), *Trichoderma saturnisporum* (Hammill 1974, Figs. 9.8-9.9), *Stachybotrys atra* (Campbell 1972), *Verticillium albo-atrum* (Buckley, Wyllie & de Vay 1969).

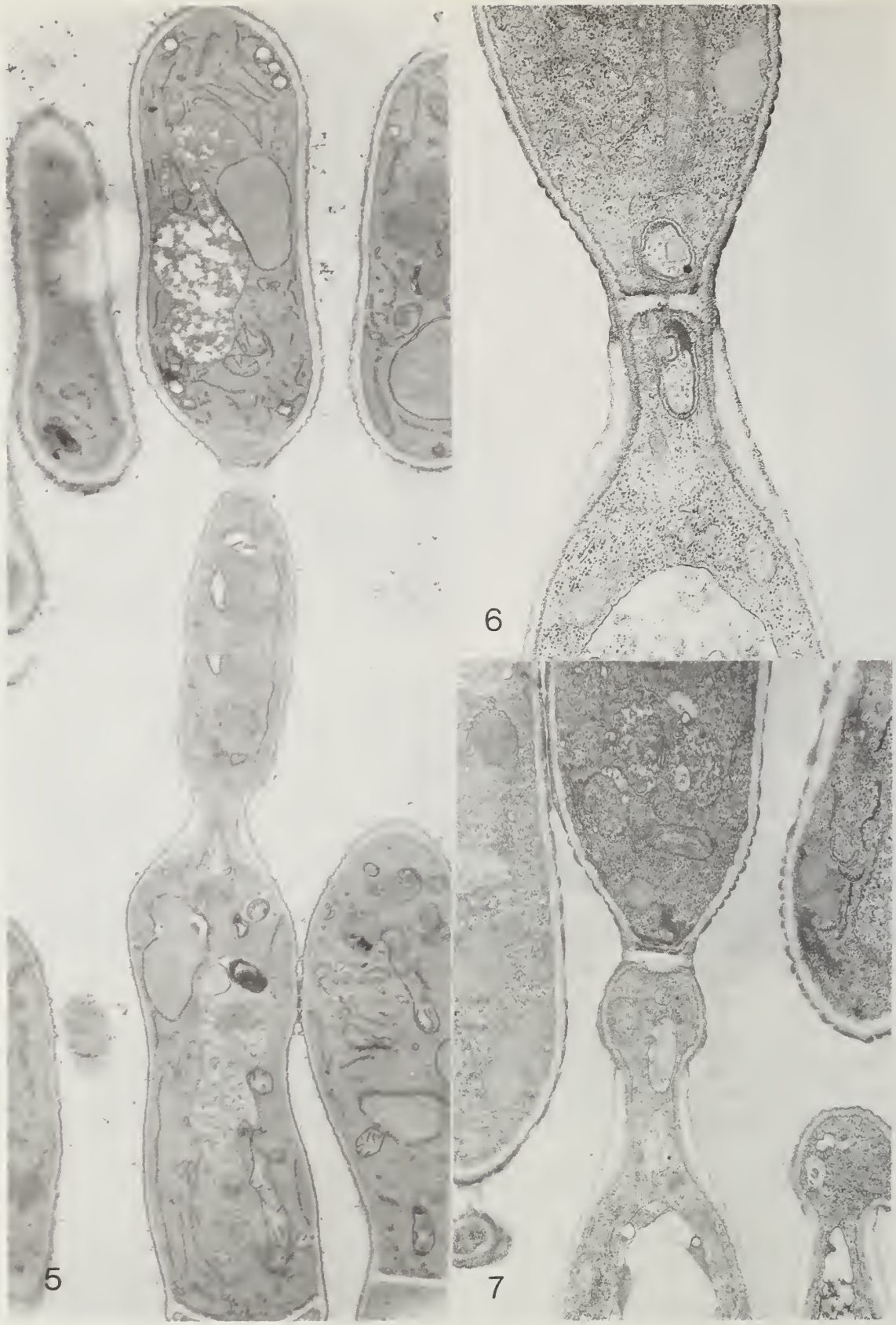
As I have stressed elsewhere (Subramanian 1972b), phialides of this kind could be thought of as annellides in which the conidia developing from successive percurrent proliferations become detached below the level of detachment of the first conidium (and not at higher and higher levels as in the typical annellide); the alternating electron dense and electron transparent striations or lamellations that are seen in the region of collarettes in phialides (Figs. 9.8, 9.9 ; see also Figs. 7.3A,B, 7.4A,B, in Subramanian 1971b; Fig. 18 in Campbell 1972; Figs. 9, 12, 13 in Hammill 1974b), in my opinion, represent marks of these percurrent proliferations.

4. Pseudosynechidic, penititunicogenous, porrectic, sympodial, solitary, glomerate, slimy, e.g., *Chloridium chlamydosporis* (Hammill 1972a, Figs. 9.10, 9.11).

Although there seems to be a fixed conidiogenous locus in these examples, further ultrastructural evidence indicates, I think, that a fixed conidiogenous locus occurs only in the case of taxa with synechidic ontogeny. On the other hand, in the forms with pseudosynechidic conidium ontogeny, this process involves percurrent proliferation in some, and sympodial proliferation in others. Obviously, therefore, the conidiogenous locus is not fixed, in such cases only appearing so under the light microscope. Marchant's (1975) ultrastructural study

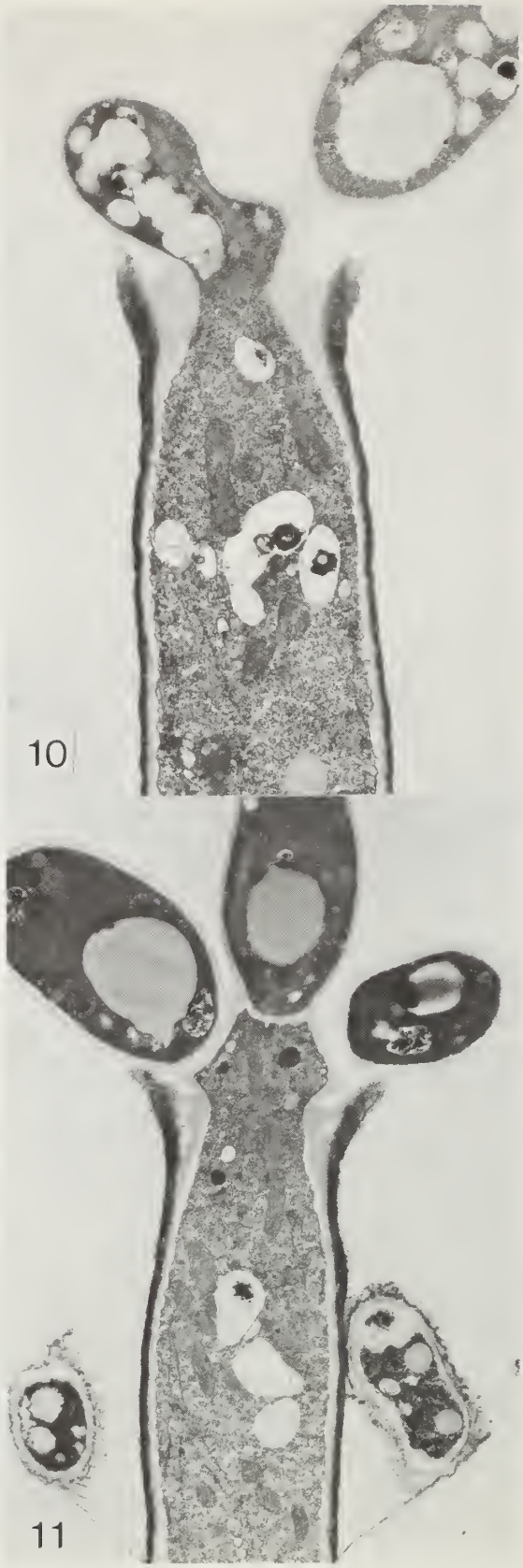


Figures 9.1-9.4 Ultrastructure of conidiogenesis in *Phialocephala dimorphospora*. Fig. 9.1, development of first conidium within apex of phialide, following cytoplasmic cleavage. x32000. Figs. 9.2-9.4, development of secondary conidia by cytoplasmic cleavage. X22500 (by permission, from Carroll & Carroll 1974).



Figs. 9.5-9.7 Ultrastructure of conidiogenesis in *Metarrhizium anisopliae*. Fig. 9.5, a phialide showing development of a true chain of two conidia in basipetal sequence x13200. Figs. 9.6-9.7, tip of phialide showing wall relationships between phialide and conidial chain: note penititunicogenous development of chain and continuity of wall layers between conidia. Fig. 9.6 x20100. Fig. 9.7 x16000. (by permission, from Hammill 1972b).

Figs. 9.8-9.9 Ultrastructure of conidiogenesis in *Trichoderma saturnisporum*: apices of phialides: note electron-dense and electron-transparent lamellations in region of collarette. Fig. 9.8 x47000. Fig. 9.9 x38500.(by permission, from Hammill 1974b).



Figs. 9.10-9.11 Ultrastructure of conidiogenesis in *Chloridium chlamydosporis*: apices of phialides showing development of conidia, which is penititunicogenous and sympodial. Fig. 9.10 x 17300. Fig. 9.11 x13000. (by permission, from Hammill 1972a).

of the genesis of the macroconidium in *Fusarium culmorum* further confirms this. According to Marchant, the first conidium "is initiated by a partition of the cytoplasm within the apex of the conidiophore [so-called phialide -- CVS] by a new membrane, destined to become the conidium plasmalemma." The early development of the conidium, including wall synthesis, is endogenous; enlargement of the conidium eventually leads to rupture of the conidiophore wall, and invariably, part of the conidiophore wall is carried away by the conidium as a cap, as illustrated by Subramanian (1971b) for *Fusarium decemcellulare*. According to Marchant, the subapical cell of the conidiophore produces a second conidium in the same way, a process that is said to be repeated, so that the conidiogenous locus is not fixed. More importantly, the conidia are endogenous, developing within the conidiogenous cells. I expect that other variations in the phialidic mode will be discovered.

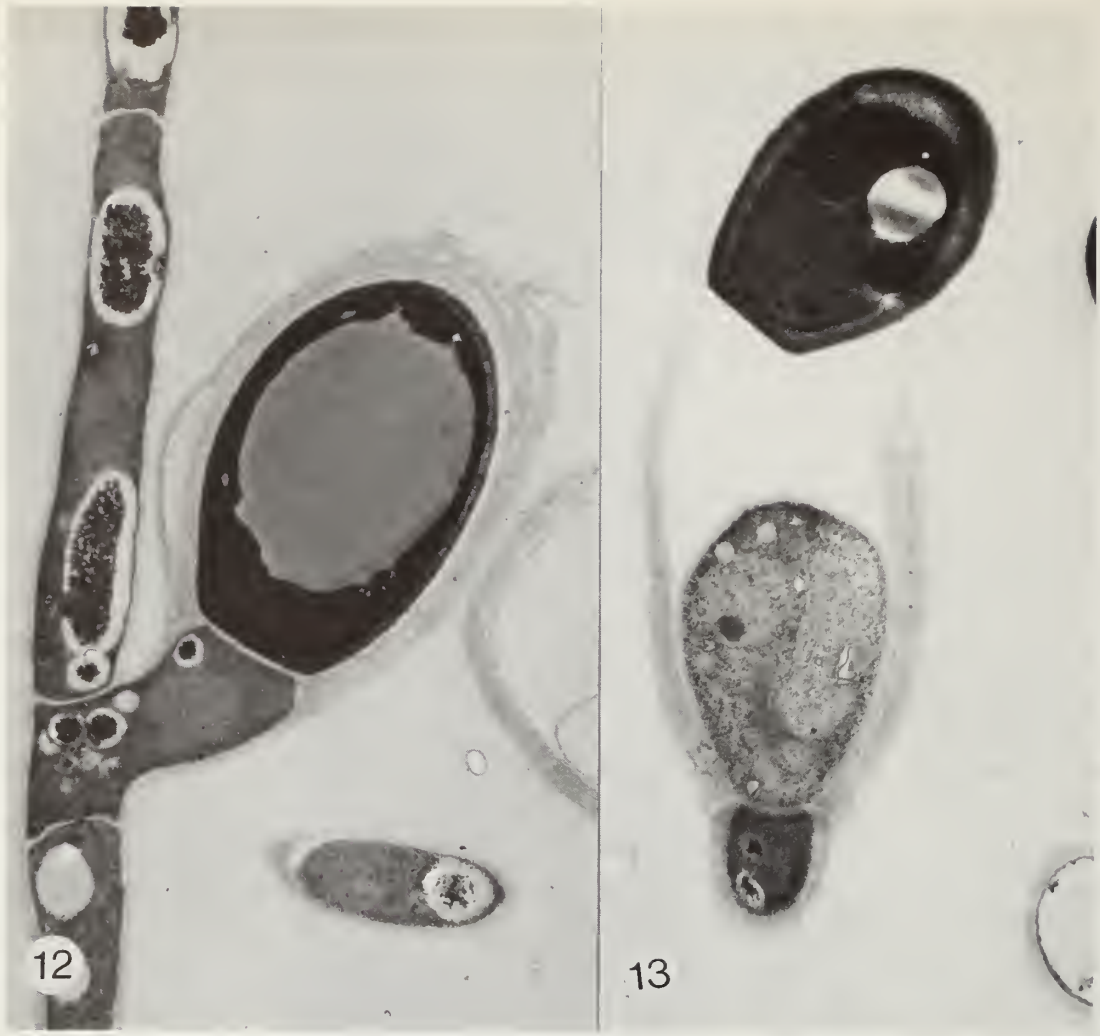
Since the concepts and terminology evolved at Kananaskis-I were largely based on information about conidiogenesis at the level of the light microscope, some doubts and difficulties have been thrown up in the wake of the new ultrastructural information that has become available (Subramanian 1972b, Hammill 1972b, 1974a, 1974b, Marchant 1975, Hanlin 1976). The question has been raised, for example, of whether conidiogenesis in *Conioscypha varia* (Figs. 9.12, 9.13) and *C. lignicola* is phialidic or annellidic (Shearer & Motta 1973). Without venturing to answer the question, one might see if the new terminology of Subramanian (1972b) could be used to describe the situation in *Conioscypha*. Conidia in *Conioscypha* are pseudosynechidic, etunicogenous, exporrectic, solitary. The conidiogenous cell proliferates percurrently, but it is not annellidic in the sense of Kananaskis-I, nor can the conidia be described as annellidic or phialidic.

There are therefore some obvious advantages to adopting the terminology suggested, if only to supplement that of Kananaskis-I. And yet I would like to inject a note of caution: although the terminology proposed can be used to describe certain modes of conidium ontogeny based on wall relationships, etc., this will not solve all our problems. The terminology is built on available information on the ultrastructure of conidiogenesis, and is at best tentative. We should see if it remains compatible with new knowledge that will become available in the next five years, after which its utility might be reviewed. I must also stress that this terminology should not be used in formal descriptions of taxa; in fact we cannot so use it, because formal descriptions may not include ultrastructural features. Also, the definitions proposed should not be modified to suit new situations. If the terminology is found wanting, we can simply say that we do not find it useful.

PHIALIDIC CONIDIOGENESIS -- SOME COMPARISONS

Among the four variations in the phialidic mode outlined above, the second, viz., the synechidic mode typical of species of *Aspergillus, Penicillium,* etc., invites comparison with that in *Oidium* spp. (conidial powdery mildews) and in *Wallemia sebi*.

In *Oidium* spp. the conidiophore arises as a lateral swelling on a hypha and gives rise to a basipetal chain of conidia as follows. A papilla arises at the apex of the conidiophore; this divides into two cells (designated A and A' in Fig. 9.14) each of which again divides into two cells, A1 and A2, and A'1 and A'2 respectively, forming a chain of four cells. In the meantime, synechidic activity at the tip of the bulbous basal cell produces a further



Figs. 9.12-9.13 Ultrastructure of conidiogenesis in *Conioscypha varia*: development of conidia within percurrently proliferating conidiogenous cell: conidia are etunicogenous and endogenous. Fig. 9.12 x8900. Fig. 9.13 x 9400. (by permission, from Shearer & Motta 1973).

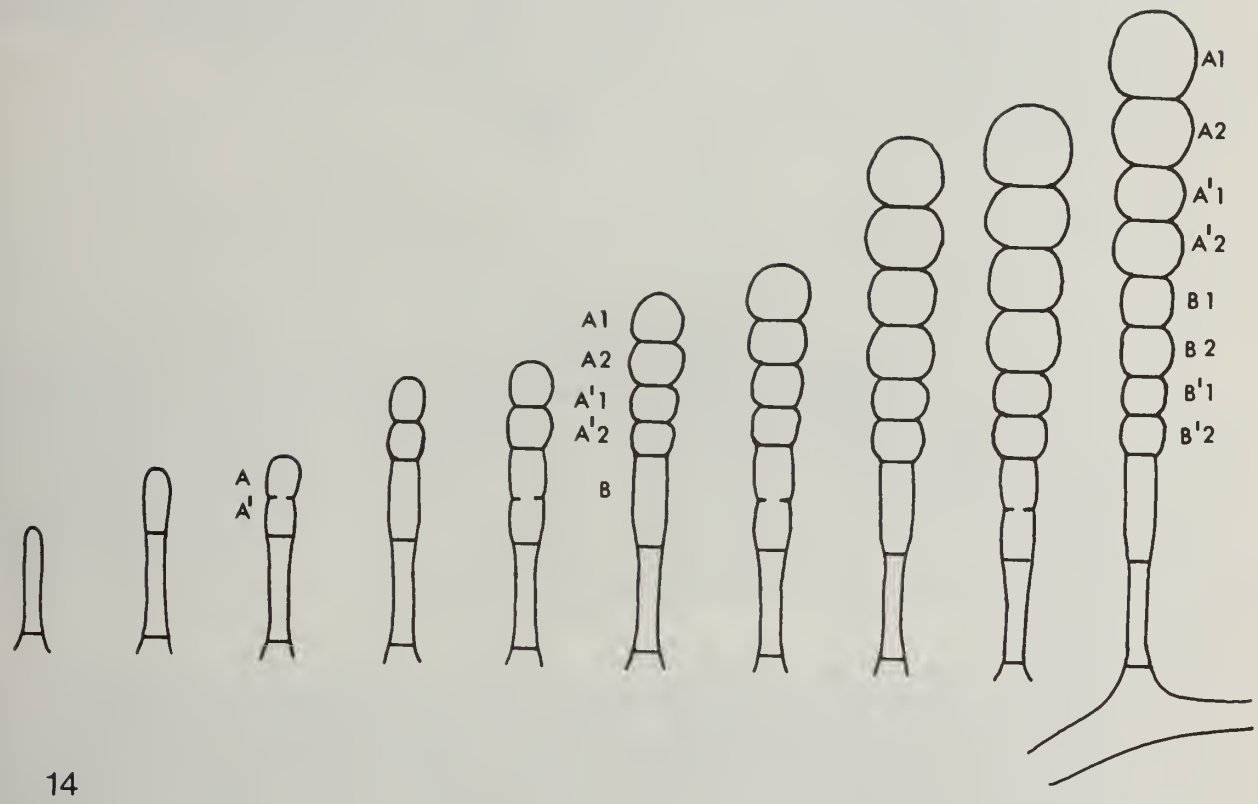


Fig. 9.14 Schematic illustration of conidiogenesis in *Oidium* spp.
For explanation see text.

length of the papilla and this is cut off as a further cell (B) which in turn divides to form four cells, B1, B2, and B'1 and B'2 in the same way. This process may continue indefinitely. The cells so cut off become transformed into conidia and swell to some extent in the process (Subramanian 1972a, Jordan 1968).

Thus, in *Oidium* spp. as well as in *Penicillium* and *Aspergillus*, the conidia are synechidic, porrectic and catenate; however, the conidia of *Oidium* spp. are totitunicogenous (holoblastic in the terminology of Kananaskis-I), while those of *Penicillium* and *Aspergillus* are penititunicogenous (=enteroblastic) (see Fig. 9.21). The similarity therefore is close: indeed, the interpretation of the phialide given by Langeron & Vanbreuseghem (1965) includes the mode of conidiogenesis of *Oidium* spp. It may be noted, in passing, that the genesis of the striate phialoconidia in *Sagrahœmala striatispora* was reported to be holoblastic (Subramanian & Pushkaran 1975), but this needs to be confirmed by electron microscope studies.

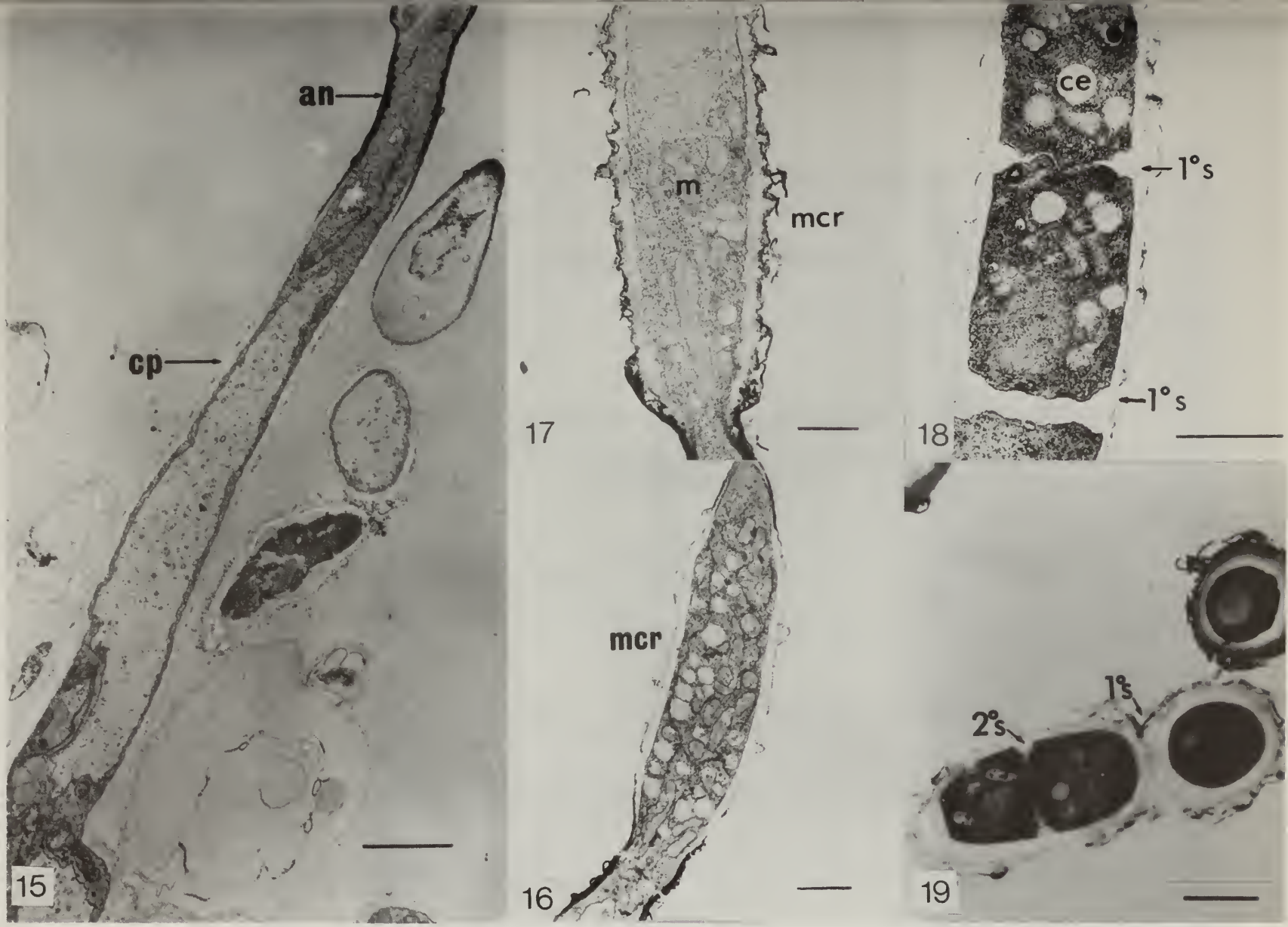
Conidiogenesis in *Wallemia sebi* follows a pattern very similar to that in *Oidium* spp. (Hill 1974, Terracina 1977). From Terracina's observations it is clear that the conidiophore has a distal constriction and a markedly thickened annulus of wall material which flares distally. During conidiogenesis, the conidiophore develops, distal to the constriction, a meristematic (synechidic) conidiogenous region, development being holoblastic. A primary septum divides the conidiogenous region into two parts, each of which then develops a secondary septum, resulting in a chain of four arthroconidia which now separate in a basipetal sequence (Figs. 9.15-9.19). The process is repeated, as is clearly shown by the time-lapse photomicrographs of Hill (1974), so that conidiogenesis is synechidic (Fig. 9.20). Terracina (1977) has further shown that the conidiophore may proliferate sympodially or percurrently, following primary conidiation.

The phialidic mode in *Aspergillus* and *Penicillium* also invites comparison with the basauxic mode typical of *Arthrinium*. In such a comparison, the conidiogenous locus of the phialide where new wall material is laid down during conidiogenesis (e.g., *Aspergillus)* corresponds to the locus of growth of the basauxic conidiophore (e.g., *Arthrinium*). The phialoconidial chain, in this comparison, would correspond to the conidiophore in species showing the basauxic condition, and the phialide of *Aspergillus* would then correspond to the conidiophore mother cell of *Arthrinium*. The chain of phialidic conidia in forms such as *Aspergillus* could then be interpreted as rather like a basauxic conidiophore undergoing basipetal conversion into a chain of gangliar conidia.

Since conidiogenesis in *Oidium* spp. and *Wallemia sebi* is very similar to that in the phialidic mode typical of *Aspergillus*, etc. (the primary difference is that the chains are holoblastic in the first two, and enteroblastic in the last), the conidial chains in these fungi can also be likened to a basauxic conidiophore that undergoes basipetal conversion into a chain of gangliar *(Oidium)* or arthric *(Wallemia)* conidia. These comparisons are depicted diagrammatically in Fig. 9.21.

PHIALIDIC AND OTHER PARAMETERS AND RELATIONSHIP TO TELEOMORPHS

Of the four variations in the phialidic mode referred to here, the second (dry phialoconidia formed in true chains) and the third (slimy phialoconidia which are glomerate or pseudocatenate) seem the most common. Since we are trying to understand the relationships of phialidic



Figs. 9.15-9.19 Ultrastructure of conidiogenesis in *Wallemia sebi*. Fig. 9.15, a conidiophore (cp) with uniformly electron-opaque annulus (an), x8400. Figs. 9.16-9.17, non-septate meristematic conidiogenous region (mcr) at tip of conidiophore. Fig. 9.16 x10000. Fig. 9.17 x11000. Fig. 9.18, conidiogenous region showing primary septa (1°s) delimiting conidial elements (ce), x17500. Fig. 9.19, conidiogenous region showing secondary septa (2°s) subdividing conidial elements into arthroconidia, x12200 (courtesy F. Terracina).

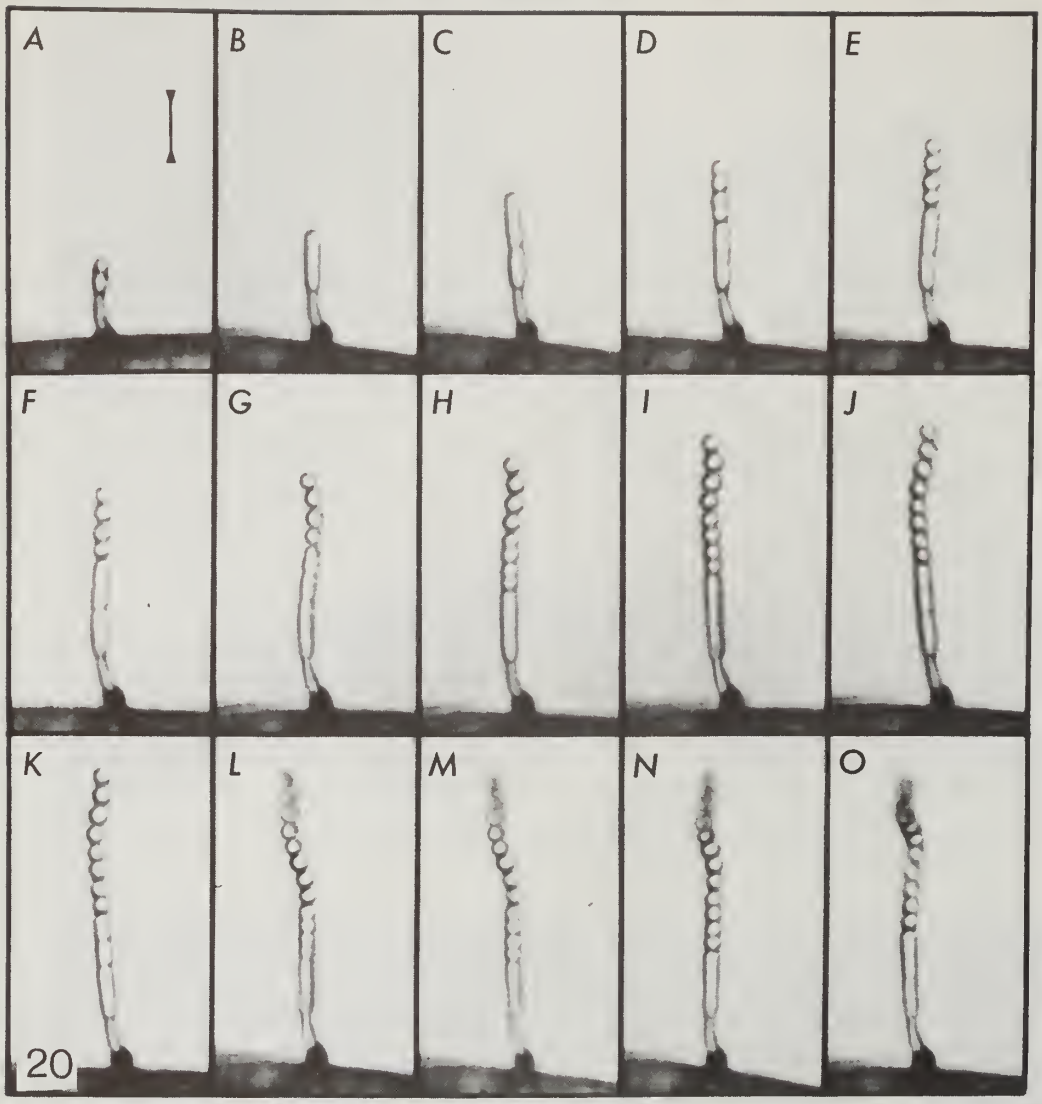


Fig. 9.20 Time-lapse sequence of conidium formation in *Wallemia sebi*. Scale = 10 µm (by permission, from Hill 1974).

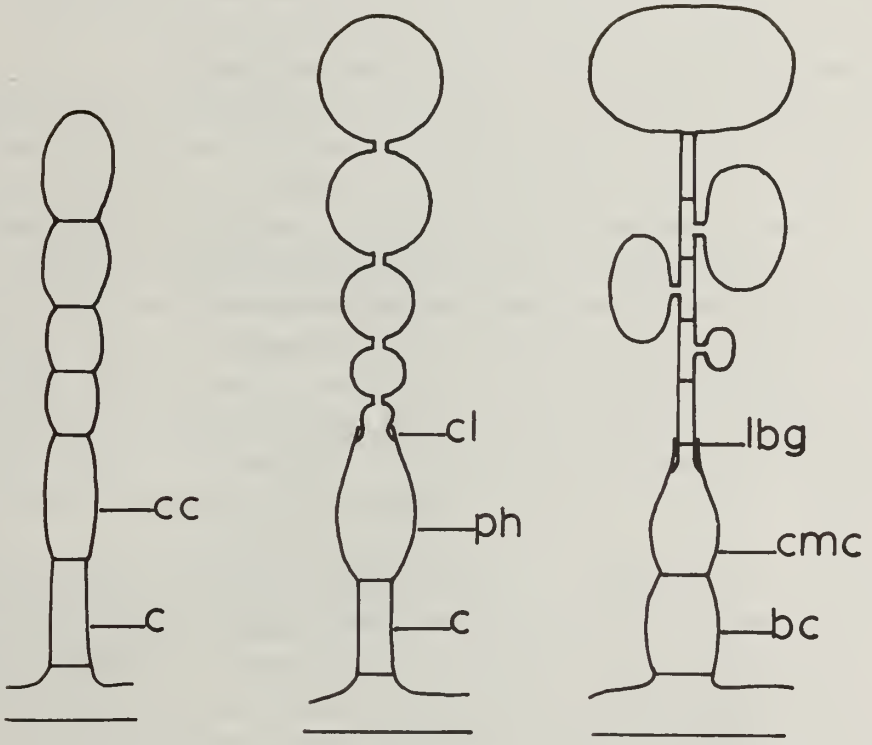


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Fig. 9.21 Diagrammatic comparison of conidiogenesis in *Oidium*, *Aspergillus* and *Arthrinium* (left to right): ph = phialide, cmc = conidiophore mother cell, c = conidiophore, bc = basal cell, cc = conidiogenous cell, cl = conidiogenous locus, lbg = locus of basauxic growth.

Hyphomycetes to their teleomorphs, we may now examine the kind of teleomorphs to which anamorphic taxa in each of these categories are currently assigned. Numerous connections are known, and for the sake of convenience and brevity our analysis will have to be at the level of the genus. Available information is given in the accompanying Tables (Tables 9.1-9.3). Table 9.1 lists genera of phialidic *non-dematiaceous* Hyphomycetes producing slimy conidia, and the genera and orders to which their teleomorphs are assigned. Table 9.2 lists phialidic *dematiaceous* Hyphomycetes producing slimy conidia, and the genera and orders to which their teleomorphs are assigned. Table 9.3 lists phialidic Hyphomycetes producing dry conidia in true chains, and the genera and orders to which their teleomorphs are assigned. The separation of non-dematiaceous forms from dematiaceous ones may surprise you, this is not as irrelevant as it may seem at first sight! In presenting this information I want to stress again that some connections are well authenticated and documented, some doubtful and requiring confirmation. Nevertheless, a few interesting points emerge:

1) The teleomorphs of non-dematiaceous Hyphomycetes with slimy conidia (which never form true chains) are largely assignable to genera in the Hypocreales, plus a few in the Clavicipitales, the Eurotiales and the Helotiales (the two connections listed for the Sphaeriales may be of doubtful validity, for reasons which I shall give below). In contrast, none of the teleomorphs of dematiaceous Hyphomycetes with slimy phialoconidia (which never form true chains) is assignable to the Hypocreales. On the other hand, many of the common and well known genera of phialidic dematiaceous Hyphomycetes have their teleomorphs in the Sphaeriales, and a few in the Pleosporales, Capnodiales, Meliolales, Microascales, Helotiales and Septobasidiales.

Ascomata of the taxa assigned to the Hypocreales are invariably bright-coloured and fleshy, and those of the Sphaeriales are typically carbonous, leathery or brittle, and dark in colour. This seems to validate the distinction between dematiaceous (brown to black) and non-dematiaceous Hyphomycetes, since the teleomorphs of dematiaceous slimy-spored taxa are in the Sphaeriales, those of their non-dematiaceous counterparts, in the Hypocreales. I consider *Gliomastix* to be the dematiaceous counterpart of *Acremonium;* the former has a teleomorph in *Wallrothiella* in the Sphaeriales, whereas the latter has its teleomorphs in some genera in the Hypocreales. Other examples may be found in Tables 9.1 and 9.2. If my conclusion is correct, one should be able to predict the group to which the teleomorphs of taxa of either of these two categories would belong. This proposition should be tested by further studies. Since the dematiaceous condition is due to production of a brown pigment or pigments (?melanin) which I believe is typical both of dematiaceous Hyphomycetes and members of the Sphaeriales, here is a biochemical parameter that may prove valuable in taxonomy. Perhaps I should add that the term 'dematiaceous' would apply only to examples where the colour is brown, and not to other colours (olive, green, etc.). To take a specific example, I would classify *Myrothecium* spp. as non-dematiaceous, and I have, in fact, done this in Table 9.1.

Thus, concerning the connections reported between *Acremonium* and *Trichosphaerella* (Sphaeriales), and between *Monocillium* and *Niesslia* (Sphaeriales), the phialoconidial anamorphs in both cases should be dematiaceous or else the connection may well be disproved by further critical study. This prediction is, of course, tentative.

Table 9.1. Genera of phialidic non-dematiaceous Hyphomycetes producing slimy conidia and the genera to which their teleomorphs are assigned.

Anamorph	Teleomorph	Order
Acremonium Link ex Fr.	*Microthecium* Corda	Hypocreales
	Mycocitrus Möller	
	Nectria Fr.	
	Neocosmospora E.F. Smith	
	Peloronectriella Doi	
Antipodium Pirozynski	*Ophionectria* Sacc.	
Calostilbella Höhnel	*Nectria* Fr.	
Ciliciopodium Corda em. Sacc.	*Nectria* Fr.	
Cylindrocarpon Wollenw.	*Nectria* Fr.	
	?*Calonectria* de Not.	
	?*Neonectria* Wollenw. (= *Nectria*)	
Cylindrocladium Morgan	*Calonectria* de Not.	
Dendrodochium Bonorden	*Nectria* Fr.	
	?*Thyronectria* Sacc.	
Flagellospora Ingold	*Nectria* Fr.	
Fusarium Link ex Fr.	*Calonectria* de Not.	
	Gibberella Sacc.	
	Griphosphaeria Höhnel	
	Monographella (Rehm) Müller	
	Nectria Fr.	
	?*Nectriopsis* Maire (= *Nectria* fide Dingley)	
	Peloronectria Möller	
	Plectosphaerella Klebahn	
Gabarnaudia Samson & Gams	*Sphaeronaemella* Karst.	
Gliocladium Corda	*Nectria* Fr.	
Heliscus Sacc. & Therry	*Nectria* Fr.	
Myrothecium Tode ex Fr.	*Nectria* Fr.	
Putagraivam Subram. & J. Bhat	*Pithambara* Subram. & J. Bhat (ined.)	
Sesquicillium Gams	*Pseudonectria* Seaver	
Stilbella Lindau	?*Byssostilbe* Petch	
	Hypocreopsis Karst.	
	Nectria Fr.	
	Pseudonectria Seaver	
	Thyronectria Sacc.	
Trichoderma Pers. ex Fr.	*Hypocrea* Fr.	
	Podostroma Karst.	
Tubercularia Tode ex Fr.	*Nectria* Fr.	
Verticillium Nees ex Wallr.	*Nectria* Fr.	

Table 9.1 (cont'd)

Anamorph	Teleomorph	Order
Volutella Tode ex Fr.	*Nectria* Fr.	Hypocreales
	Pseudonectria Seaver	
Sphacelia Lév.	*Claviceps* Tul.	Clavicipitales
	Epichloe (Fr.) Tul.	
Verticillium Nees ex Wallr.	?*Cordyceps* (Fr.) Link	
	?*Torrubiella* Boudier	
Acremonium Link ex Fr.	*Emericellopsis* van Beyma	Eurotiales
	Levispora Routien	
	Mycoarachis Malloch & Cain	
	Nigrosabulum Malloch & Cain	
Gliocladium Corda	*Lilliputia* Bond. & Pat.	
Stilbella Lindau	*Emericellopsis* van Beyma	
Acremonium Link ex Fr.	?*Trichosphaerella* Bomm., Rouss. & Sacc.	Sphaeriales
?*Monocillium* Saksena	*Niesslia* Auersw.	
Sesquicillium Gams	*Gnomonia* Ces. & de Not.	
Myrothecium Tode ex Fr.	*Gelatinodiscus* Kanouse & A.H. Smith	Helotiales
Stilbella Lindau	*Helotiella* Sacc.	

Table 9.2. Genera of phialidic dematiaceous Hyphomycetes producing slimy conidia and the genera to which their teleomorphs are assigned.

Anamorph	Teleomorph	Order
Catenularia Grove ex Sacc.	*Chaetosphaeria* Tul.	Sphaeriales
Chloridium Link	*Chaetosphaeria* Tul.	
Cladorrhinum Sacc. & Marchal	*Apiosordaria* Arx & Gams	
Codinaea Maire	*Chaetosphaeria* Tul.	
Gliomastix Gueguen	*Wallrothiella* Sacc.	
Gonytrichum Nees & Nees	*Melanopsammella* Höhnel	
Menispora Pers. ex Chev.	*Chaetosphaeria* Tul.	
Phialophora Medlar	*Coniochaeta* (Sacc.) Massee	
	Gaeumannomyces Arx & Olivier	
Sporoschisma Berk. & Br.	*Melanochaeta* Müller	
	Chaetosphaeria Tul.	
Stachybotrys Corda	*Melanopsamma* Niessl	
Zanclospora Hughes & Kendrick	*Chaetosphaeria* Tul.	
Koorchaloma Subram.	gen. nov. (Nag Raj, ined.)	
Aureobasidium Viala & Boyer	*Xenomeris* Sydow	Pleosporales
	Guignardia Viala & Rivaz	
Hormisciomyces Bat. & Nascim.	*Euantennaria* Speg.	
Capnophialophora Hughes	*Limacinia* Neger	Capnodiales
	Metacapnodium Speg.	
	Ophiocapnocoma Bat. & Cif.	
Plokamidomyces Bat.	*Trichopeltheca* Bat., Costa & Cif.	?Capnodiales
Capnophialophora Hughes	*Strigopodia* Bat.	Meliolales
Chalara (Corda) Rabenh.	*Cryptendoxyla* Malloch & Cain	Eurotiales
Chalara (Corda) Rabenh.	*Ceratocystis* Ell. & Halst.	Microascales
Phialographium Upadh. & Kendrick	*Ceratocystis* Ell. & Halst.	
Cystodendron Bubak	*Bisporella* Sacc.	Helotiales
Haplographium Berk. & Br.	*Hyaloscypha* Boud.	
Phialophora Medlar	*Ascocoryne* Groves & Wilson	
	Mollisia (Fr.) Karst.	
	Pyrenopeziza Fuckel	
Harpographium Sacc.	*Septobasidium* Pat.	Septobasidiales

Table 9.3. Genera of phialidic Hyphomycetes producing dry conidia in true chains and genera to which their teleomorphs are assigned.

Anamorph	Teleomorph	Order
Aspergillus Mich. ex Fr.	*Chaetosartorya* Subram.	Eurotiales
	Cleistostroma Muthappa & Rajendran (ined.)	
	Dichlaena Dur. & Mont.	
	Edyuillia Subram.	
	Emericella Berk. & Br.	
	Eurotium Link ex Fr.	
	Fennellia Wiley & Simmons	
	Hemicarpenteles Sarbhoy & Elphick	
	Hemisartorya Rai & Chowdh.	
	Neosartorya Malloch & Cain	
	Petromyces Malloch & Cain	
	Sclerocleista Subram.	
Paecilomyces Bain.	*Byssochlamys* Westling	
	?*Dactylomyces* Sopp	
	Talaromyces Benjamin	
Penicillium Link ex Fr.	*Eupenicillium* Ludwig	
	Hamigera Stolk & Samson	
	Penicilliopsis Solms-Laubach	
	Talaromyces Benjamin	
	?*Trichocoma* = Trichoskytale Corda	
Raperia Subram. & Rajendran	*Warcupiella* Subram.	
Sagrahamala Subram.	?*Cephalotheca* Fuckel	
	Sagenoma Stolk & Orr	
Gibellula Cavara	*Torrubiella* Boud.	Clavicipitales

2) A second point that emerges from the present analysis is the fact that most phialidic Hyphomycetes producing dry conidia in true chains have teleomorphs in the Eurotiales, with the exception of *Gibellula*, which has teleomorphs in *Torrubiella* in the Clavicipitales. The significance of exceptions to this is not clear yet, but it may indicate that the Eurotiales as currently circumscribed are heterogeneous -- a point I wish to expand upon.

The correlation that links species producing dry phialoconidia in true chains with the Eurotiales is of special interest. Campbell (1975) and Hawes & Beckett (1977a) expressed doubts about the taxonomic usefulness of the distinction between true chains and false chains. I still believe, however, that this distinction is not only valid in itself, but is reinforced by a consideration of anamorph-teleomorph relationships. For instance, the distinction between *Penicillium* and *Gliocladium* -- genera which I presume we accept -- is that in the former the conidia are dry and form true chains, whereas in the latter they are slimy and do not form true chains, but are produced singly and successively in basipetal sequence, and slime down. The fact that the teleomorphs of *Gliocladium* are in the Hypocreales and those of *Penicillium* are not, I think, lends validity to the distinction of these two Hyphomycete genera, apart from the differences in their conidium ontogenies. Other examples will emerge from a perusal of Tables 9.1-9.3. In the case of the *Chalara* state of *Ceratocystis adiposa*, Hawes & Beckett (1977a:261) refer to "two distinct chain types ... the easily fragmented type, composed of hyaline, doliiform conidia" and "the persistent chains ... surrounded by a sheath". Their acceptance of the difference between these two types seems unmistakable. What is particularly interesting is that *C. adiposa* produces both types, but the distinction is no less important because of this association. I think the distinction between true and false chains which I stressed at Kananaskis-I has now received further scrutiny and confirmation (Subramanian 1972a, Subramanian & Pushkaran 1975, Roquebert 1976, Hawes & Beckett 1977a,b). On the question of whether this has taxonomic value or not we may differ, but my opinion is that it has not only morphological and biological significance, but is of special relevance in any taxonomic system that attaches importance to patterns in conidiogenesis.

The correlation here emphasized between the Eurotiales and anamorphs which produce dry phialoconidia in true chains, is only tentative, and hinges on our belief that the genera in the Eurotiales listed in Table 9.3 are a homogeneous group. In the case of other groups also, e.g., the Hypocreales, homogeneity of the group is implied. It is not the purpose of this presentation to discuss the Eurotiales or the Hypocreales in any detail, but it is pertinent to refer to our recent work on developmental morphology, which has shown that, even within the Eurotiales, widely differing patterns of development occur.

DEVELOPMENTAL MORPHOLOGY OF THE EUROTIALES -- AN ANALYSIS

The simplest type of ascoma organization is what we see in *Edyuillia*, in which only a cluster of a few asci is produced per ascogonium (Subramanian & Rajendran 1977a).

In the case of *Byssochlamys* numerous asci are produced per ascogonium and they lie scattered in an ascoma which has no peridium (Rosenbaum 1944, Kuehn 1957, Subramanian & Rajendran 1979a).

In *Eurotium* (de Bary 1887, Dangeard 1907, Frazer & Chambers 1907, Dale 1909), *Neosartorya* (Olive 1944, Malloch & Cain 1972) and *Chaetosartorya* (Subramanian & Rajendran 1979b) the asco-

ma is known as a cleistothecium. Each ascoma is the product of usually a single ascogonium, and in all three genera the peridium is cellular or pseudoparenchymatous. These three genera, therefore, appear to be closely related. The peridium consists of a single layer of cells in *Eurotium* and *Chaetosartorya*, and of three to five layers of cells in *Neosartorya*. The peridium in *Chaetosartorya* has hyphal projections, but these are not found in *Eurotium*.

In the genera *Warcupiella* and *Hamigera* the mature ascoma with its scattered asci is enveloped by a felt of hyphae. If one does not know the sequence of development of the ascoma, it may be considered to be a cleistothecium with a prosenchymatous peridium. However, from our study (Subramanian & Rajendran 1979c), it is clear that the so-called cleistothecium is in fact an ascostroma in which several ascogonia develop, each ascogonium giving rise to croziers and asci which come to lie scattered within the stroma surrounded by part of the original stroma -- the so-called 'peridium'. If we consider the products of development of a single ascogonium as an ascoma, in the case of *Warcupiella* and *Hamigera* we have several ascomata developing within the stroma, but none of them develops a peridium of its own. On the other hand, they become confluent and their precise origin cannot be determined without careful study of their development. In other words, the so-called cleistothecium of *Warcupiella* and *Hamigera* is considered to be an ascostroma in which several non-peridiate ascomata develop.

In the case of *Thermoascus* the development of the ascoma is similar to that of *Warcupiella* and *Hamigera* in that several ascogonia develop in a prosenchymatous ascostroma and each ascogonium gives rise to asci, so that here also, several non-peridiate ascomata develop within a prosenchymatous stroma (Subramanian & Rajendran 1979d). However, there is one important difference between *Thermoascus* on the one hand, and *Warcupiella* and *Hamigera* on the other. In *Thermoascus* the peripheral part of the stroma does not remain prosenchymatous, but gradually becomes pseudoparenchymatous even during early stages of development of the ascogonia, asci, etc. It is this pseudoparenchymatous stromal tissue that is usually interpreted as a peridium. As understood here, therefore, *Warcupiella*, *Hamigera* and *Thermoascus* develop their asci in 'locules' formed in a stroma.

In *Fennellia* several ascogonia arise in a prosenchymatous stroma, and each ascogonium gives rise to an ascoma with a pseudoparenchymatous peridium (Subramanian & Rajendran 1979e). Thus, *Fennellia* resembles *Warcupiella*, *Hamigera* and *Thermoascus* in that several ascogonia develop in a prosenchymatous stroma; but then the ascoma arising from each ascogonium develops a distinct pseudoparenchymatous peridium so that its identity is maintained. In other words, the asci develop within peridiate ascomata in a stroma (and not in locules, like *Warcupiella*, *Hamigera* and *Thermoascus*). Another unique feature of *Fennellia* is the conspicuous occurrence of hülle cells enveloping the groups of ascomata. In producing hülle cells, it resembles *Emericella*. Unfortunately, we do not know whether the so-called cleistothecium of *Emericella* develops in the same way as the ascoma of *Fennellia*, or like those of *Eurotium*, *Neosartorya* or *Chaetosartorya*, or in some other way. When we have more definite information on the developmental morphology of *Emericella variecolor*, the type species of the genus *Emericella*, we can say something more definite about this.

Petromyces resembles *Fennellia* in that several ascomata develop within a stroma, each with its own pseudoparenchymatous peridium. However, the stroma is not prosenchymatous, as in *Fennellia*, but pseudoparenchymatous even in the very early stages (Subramanian & Rajendran 1979f). There are no hülle cells in *Petromyces*.

Thus, we have stromatic and non-stromatic taxa in the Eurotiales. *Eurotium*, *Neosartorya* and *Chaetosartorya* are non-stromatic; one might refer to their ascomata as true cleistothecia. *Warcupiella*, *Hamigera* and *Thermoascus* are ascostromatic forms which develop their asci within 'locules' in a stroma which in all three genera is prosenchymatous, part of the peripheral stroma becoming pseudoparenchymatous during later development in *Thermoascus*, the prosenchymatous condition persisting in *Warcupiella* and *Hamigera*.

Eupenicillium is ascostromatic (Brefeld 1874), the asci developing in a 'locule' in a stroma, but in this case the stroma is pseudoparenchymatous from the start.

Fennellia and *Petromyces* fall into a third category. Both are ascostromatic, the stroma being prosenchymatous in the former, but pseudoparenchymatous in the latter. In both genera the asci develop within peridiate ascomata within the stroma.

The following tentative key to some of the genera discussed here (see also Figs. 9.22, 9.23) is intended to summarize the main points mentioned above.

A. Ascoma absent, asci not evanescent ..... *Edyuillia*
AA. Ascoma present, asci evanescent ..... B
B. Stroma absent C
BB. Stroma present ..... F
C. Ascoma without peridium ..... *Byssochlamys*
CC. Ascoma with peridium ..... D
D. Peridium single-layered ..... E
DD. Peridium 3-5-layered ..... *Neosartorya*
E. Peridium without appendages or hairs ..... *Eurotium*
EE. Peridium with appendages or hairs ..... *Chaetosartorya*
F. Asci developing in locules in the stroma ..... G
FF. Asci developing in peridiate ascomata within the stroma I
G. Stroma prosenchymatous throughout development ..... H
GG. Stroma prosenchymatous to begin with, but peripherally becoming pseudoparenchymatous later ..... *Thermoascus*
GGG. Stroma pseudoparenchymatous throughout ..... *Eupenicillium*
H. Ascogenous hyphae not prominent; anamorph *Raperia* ..... *Warcupiella*
HH. Ascogenous hyphae prominent; anamorph *Penicillium* ..... *Hamigera*
I. Stroma prosenchymatous; hülle cells present ..... *Fennellia*
II. Stroma pseudoparenchymatous; hülle cells absent ..... *Petromyces*

In this resumé of our knowledge of the developmental morphology of some genera of the Eurotiales, we have concentrated on the type species of the various genera, and our analysis clearly shows that, despite similarities, taxa currently disposed in this group differ significantly in their developmental morphology. Indeed, some differences are of such magnitude as to raise doubts about the relationship which their present disposition implies. The main theme that has emerged from our analysis, in other words, is heterogeneity : heterogeneity of the phialidic mode, heterogeneity in developmental morphology of the teleomorph, and the differing correlation-patterns of the two. Not that the similarities which impelled us to bring

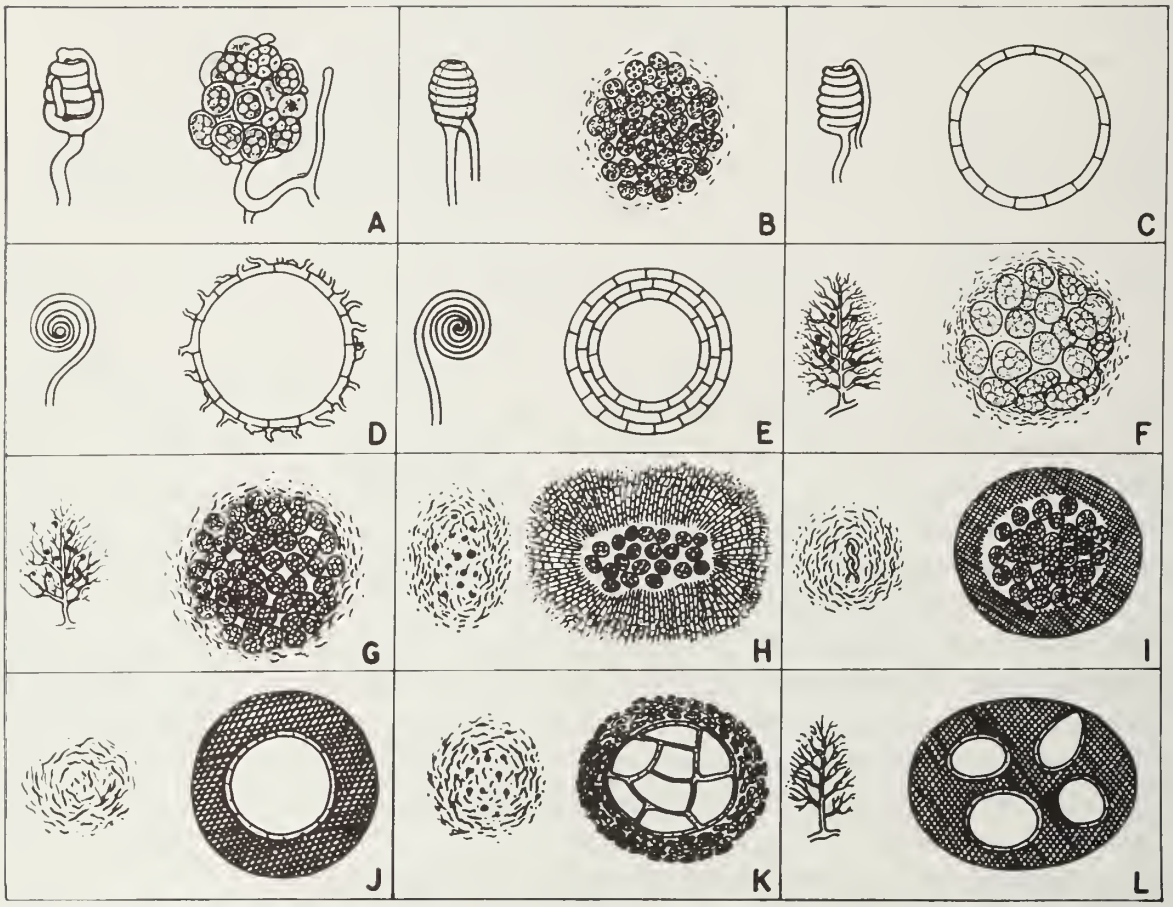

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Fig. 9.22 Diagrams to show structure of ascoma and ascoma-initiating structure (ascogonium, etc.) in twelve genera of Eurotiales. A, *Edyuillia;* B, *Byssochlamys;* C, *Eurotium;* D, *Chaetosartorya;* E, *Neosartorya;* F, *Warcupiella;* G, *Hamigera;* H, *Thermoascus;* I, *Eupenicillium;* J, *Cleistostroma;* K, *Fennellia;* L, *Petromyces.* For explanation see text.

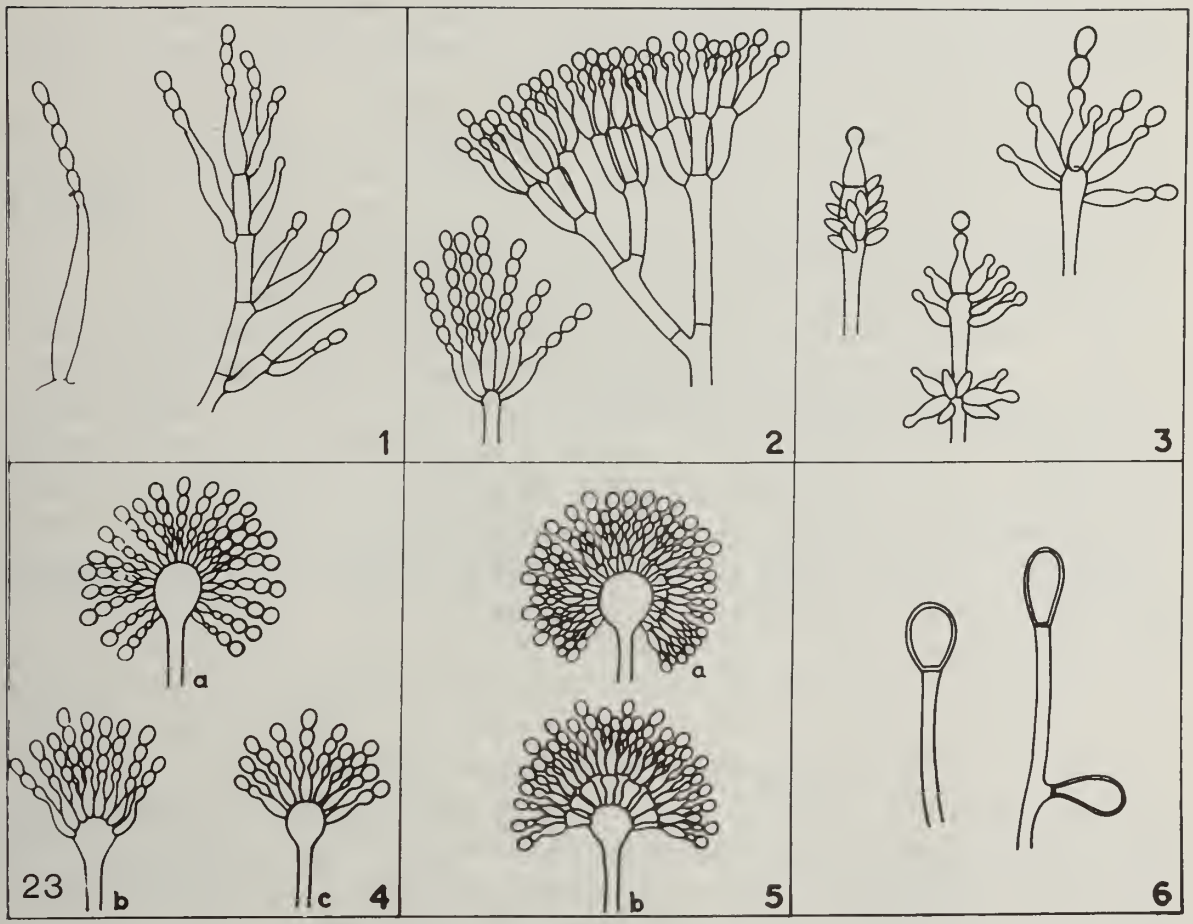

Fig. 9.23 Diagrams to show the structure of the anamorphs of the teleomorphs in Fig. 9.22. 1, *Paecilomyces;* 2, *Penicillium;* 3, *Raperia;* 4,5, *Aspergillus;* 6, anamorph of *Thermoascus.*

these taxa together in the Eurotiales are unimportant. Far from it; but the differences are equally significant, and this may well apply to the Hypocreales and other orders as well. One approach to determining relationships is developmental morphology, and the need to study thoroughly as many taxa as possible from this point of view is obvious. Our knowledge of the developmental morphology of the anamorphs and their teleomorphs in the Eurotiales, and indeed of other Ascomycotina, is still incomplete and inadequate. This lacuna will have to be filled, and in our effort to do this, we must accord equal importance to features of anamorph and teleomorph. I believe that further work will lead to a redisposition of taxa in the Eurotiales. As far as the phialoconidial states are concerned, one might say that those that produce true chains of dry conidia are more closely related to each other than those that produce slimy conidia. Obviously, we have both elements in the Eurotiales as currently delimited, additional evidence for the heterogeneity already referred to. In the case of the Hypocreales, on the other hand, so far as we know, the conidia never form true chains.

The distinction between dematiaceous and non-dematiaceous phialidic Hyphomycetes which I have introduced here is another aspect of the question, but this is not new; it is, in fact, Saccardoan. I have stressed it because I think it still has relevance. The fact that we have two recent books on *Dematiaceous* Hyphomycetes (Ellis 1971, 1976) is a reminder that the concept persists. I know that generalizations can be dangerous, but they are presented here only tentatively. If what I have said stimulates new thinking, and eventually contributes to a better understanding of the problem, I shall feel more than satisfied.

I am grateful to my good friends who have very generously supplied and permitted inclusion of electron micrographs or other material in this paper.

DIALOGUE FOLLOWING DR. SUBRAMANIAN'S PAPER

Dr. Nag Raj opened this discussion by showing superb photomicrographs of a connection he had recently made between a species of *Koorchaloma* (a dematiaceous, slimy-spored, phialidic Hyphomycete) and its teleomorph, an undescribed genus of the Sphaeriales. He suggested that this was one more piece of confirmatory evidence for Dr. Subramanian's thesis.

MALLOCH: I'd like to comment on your suggestion that *Warcupiella* and *Hamigera* be amalgamated. Something similar might also happen to *Hemicarpenteles* and *Eupenicillium:* one has a *Penicillium* anamorph and the other an *Aspergillus* anamorph. But there has been an unfortunate tendency to consider the cleistothecial fungi as more like form-genera, because they are so reduced, and to synonymize them when it isn't necessary. In the cases I have just mentioned, the different anamorphs show that, despite the close similarity of the teleomorphs, they actually belong to two different evolutionary lines -- albeit lines that have undergone parallel evolution -- and they should be maintained as separate entities. I will discuss more of these parallel lines in my paper.

SUBRAMANIAN: I did not say that *Warcupiella* and *Hamigera* should be amalgamated. What I did say was that their structure and developmental morphology are very similar, and when the developmental morphology of a larger number of taxa in the Eurotiales is elucidated it might turn out that we may have to reduce to synonymy names which may be superfluous on this basis. In fact, I have retained both names.

VON ARX: I agree with most of the points Dr. Subramanian has made. He has shown that the Eurotiaceae differ from the ostiolate pyrenomycetes by more than the absence of an ostiole in the ascoma. Some Eurotiaceae do not produce phialides; for example, some species of *Thermoascus*. That is why I do not differentiate between *Thermoascus* and *Dactylomyces*. We also use features of the asci. In *Neosartorya* they are catenulate, while in *Hamigera* they are never in chains. These are very useful supplementary characters. I also would prefer to maintain separate Ascomycete genera for the teleomorphs of *Penicillium* and *Aspergillus*.

SUBRAMANIAN: What do the experts think of the Eurotiales, in the light of developmental and other information?

MALLOCH: I'll have a lot to say about them in a few minutes, but for now I'll simply say that I think the group is very heterogeneous -- it comprises several convergent lines of evolution.

SUBRAMANIAN: There are some elements that appear to be intermediate between the Eurotiales and Hypocreales.

VON ARX: I do not know any such intermediates between Sphaeriales and Eurotiaceae (I use Eurotiaceae instead of Eurotiales, and Sphaeriales instead of Hypocreales).

SUBRAMANIAN: What I mean is that the Eurotiales with hyaline slimy phialoconidia may prove to be more closely related to the Hypocreales.

KENDRICK: Dr. Subramanian makes the point in his Table 9.1. There's a nice long list of Hypocreales with hyaline, slimy phialoconidia. But he also lists some Eurotiales there. Presumably these are the aberrant forms, because the main body of Eurotiales, with dry phialoconidia, are listed in Table 9.3.

VON ARX: Because there are so many intermediate forms, I have never accepted the distinction between Sphaeriales and Hypocreales and Diaporthales. To me they are all Sphaeriales. This makes things much simpler and more natural.

KENDRICK: That idea would tend to devalue Dr. Subramanian's distinction between the hyaline and dematiaceous slimy phialoconidia.

SUBRAMANIAN: Perhaps, but *Acremonium* sensu Gams contains both hyaline and dematiaceous forms, and forms which produce dry conidia in chains as well as those having slimy conidia. I can't accept either of those taxonomic conclusions.

KENDRICK: Neither can I. *Gliomastix* for example, is an eminently recognizable genus, easily distinguished from *Acremonium*. Perhaps at this point we could have a definite statement from someone about the aberrant Eurotiales -- *Emericellopsis, Levispora, Mycoarachis, Nigrosabulum, Trichocoma* and *Lilliputia*. Would they belong to Table 9.3 according to anyone here?

VON ARX: *Emericellopsis* in my opinion is best classified in the Hypocreaceae. That fits in with Subramanian's ideas.

MALLOCH: I place *Levispora* in synonymy with *Pseudeurotium*. *Emericellopsis, Mycoarachis,* and *Nigrosabulum* all belong with *Pseudeurotium* in the family Pseudeurotiaceae. *Trichocoma* has a *Penicillium* anamorph, and belongs elsewhere, in Table 9.3. Kobayasi & Tubaki have suggested that *Trichocoma* is congeneric with *Talaromyces*. *Lilliputia* I would put in the Nectriaceae.

VON ARX: One genus has been forgotten here; *Sphaeronaemella* with a *Gabarnaudia* anamorph.

The ascomata are colourless, sometimes ostiolate, sometimes non-ostiolate. Should this genus be classified in the Hypocreaceae or Eurotiaceae?

MALLOCH: I'd put it in the Nectriaceae. Samson's illustrations of the *Gabarnaudia* are extremely similar to some of Booth's illustrations of *Nectria* conidial states.

VON ARX: Yes, I'd agree; it could go in the Hypocreaceae (= Nectriaceae).

KENDRICK: Would someone venture an opinion on the Clavicipitales listed here: how close are they to the Hypocreales?

MÜLLER: The ascus is very different in the Clavicipitales, with a thick chitinous apex pierced by a fine canal. I don't think the Clavicipitales are closely related to the Hypocreales.

VON ARX: But I would still put them in the Sphaeriales, which includes the Hypocreaceae, Sphaeriaceae and Diaporthaceae which in France and in North America are usually given Ordinal rank. To the connections given here must be added *Epichloë*, which like *Claviceps*, has a *Sphacelia* anamorph. The *Verticillium* listed as an anamorph of *Cordyceps* and *Torrubiella* is questionable.

KENDRICK: I'm trying to clean up the odd groups. Now we've got rid of some of the exceptions. We seem to have dealt fairly satisfactorily with the Eurotiales, and Dr. Von Arx deals with the Clavicipitales and Sphaeriales by lumping them with the Hypocreales.

MALLOCH: The really simple or reduced anamorphs like *Acremonium* or *Verticillium* are so polyphyletic that we must be extremely cautious about basing any taxonomic decisions on them.

SUBRAMANIAN: The most important separation I would like to see recognized is that between the slimy conidia that don't form true chains, and those which are dry and in true chains.

VON ARX: Within the unitunicate pyrenomycetes (I use that term rather than Sphaeriales), I know three different groups. Anamorphs of the first have phialides and may be Hyphomycetes or Coelomycetes. Anamorphs of the second are blastic-sympodial (Xylariaceae). Anamorphs of the third group have large conidia with a truncate base -- *Coryneum*-like, *Seimatosporium*-like, *Pestalotia*-like. There may be some intermediates, but these three groups are recognizable and natural, in my opinion. But more than half the genera have *no* conidial states, and this creates a problem.

CARMICHAEL: The *Scopulariopsis* associated with *Wardomyces dimerus* doesn't fit into your divisions. It is annellidic, producing 2-celled conidia in chains which have a common, continuous outer wall. As soon as you develop a nice scheme, a fungus comes along and spoils it.

VON ARX: Another *Wardomyces* species is known to be an anamorph of a member of the Microascaceae, a small fourth group of the unitunicate pyrenomycetes, which often includes *Scopulariopsis* anamorphs.

SUBRAMANIAN: The fungi are not there to listen to us: we are here to listen to them.

MADELIN: I think there is a difference in attitude between the taxonomists and the comparative morphologists. The taxonomist is inevitably looking for subtle distinctions which will allow him to distinguish his taxa. The comparative morphologist is trying to establish basic similarities, and tends to feel that differences are often rather secondary. These opposite attitudes seem to surface when we deal with the distinction between slimy conidia and dry conidia in chains which may or may not be true chains. I appreciate that

as a taxonomist, Dr. Subramanian feels there are distinct entities defined by true chain versus false chain; but when one looks at these very closely under the EM, it is often very difficult to make that distinction. The so-called true and false chains *may* be fundamentally different in some way, but I am not convinced that there is in fact a continuous wall uniting the true chain. There may be a dried-out pellicle, but there is certainly not the kind of basic difference Dr. Subramanian is talking about.

KENDRICK: Dry chains are often extremely hydrofuge, and there must therefore be a waxy layer at the surface of the conidia. It may be this which gives the impression of an extra wall.

Looking again at Table 9.1, I note that *Myrothecium* and *Stilbella* are noted as having teleomorphs in the Helotiales. I know both of these genera as anamorphs of Nectrioid Hypocreaceous fungi. Would anyone like to comment?

MÜLLER: Phialidic anamorphs are very common throughout the Helotiales. But it is rather boring -- they are mostly *Acremonium*-like or *Phialophora*-like.

VON ARX: The asci in the Helotiales are very similar to those of the Sphaeriales and I consider these Orders to be related. The Helotiales are the discomycetous counterparts of the Sphaeriales.

WATLING: I'd like to draw attention to a unique example in Table 9.2. *Harpographium* is the anamorph of *Septobasidium*. This is a connection that has been conclusively established by Cole & Talbot (1977) and I'd like to point out how variable this anamorph is. Some areas of a synnema of the teleomorph can bear simple phialides, while other areas produce complex phialophores. Couch (1938) lists many anamorphs for species of *Septobasidium* but he does not establish organic connections, and some of these may actually be secondary colonizers of the *Septobasidium* hymenium.

Dr. Subramanian has examined a range of teleomorphs in the light of their associated phialidic anamorphs; now Dr. Malloch will discuss some anamorphs as illuminated by recently developed concepts in the evolution and classification of their teleomorphs. Clearly, two-way communication is opening up.....

10
Plectomycetes and Their Anamorphs

D. Malloch

Mycologists have always tended to study the sexual and asexual forms of fungi as separate entities, in spite of the fact that connections between these forms have been known to exist since the days of de Bary (1854) and Tulasne & Tulasne (1861-1865). A dual system of nomenclature allowing two names for one and the same fungus still exists today and is given full recognition in Art. 59 of the Rules of Botanical Nomenclature.

The reasons for this situation are difficult to assess, but probably involve at least two long-standing impediments. First of all there is the practical problem of human intellectual limitations. It is just beyond most of us to master sufficient knowledge in two independent fields to bring them together. Secondly, there is a firm belief among most taxonomists that the only features reliable enough to indicate phylogenetic relationships are those involving sexually produced structures. In the case of Ascomycetes, this means ascomata, asci, and ascospores.

Taxonomists resemble the characters they most value: they are conservative. New characters of a non-sexual nature are not readily accepted, and those who propose them are considered to be a little rash. However, such criteria as vegetative structures, ecology, parasitic relationships, and biochemistry are beginning to make themselves felt, often in a way that is less painful than the traditionalist might have expected. Most often, when new characters are put to use, perhaps even run through a computer, the taxonomist is surprised to find that his original schemes are confirmed, or even strengthened.

The use of asexual fruiting structures (anamorphs) as taxonomic characters in the Ascomycetes is increasing. In some cases this practice is almost traditional, as with Ascomycetes having *Aspergillus* forms of sporulation. In this group the sexually determined structures were considered to be of secondary importance to the asexual ones, until Benjamin (1955) re-examined the whole group and pointed out certain inconsistencies. Hughes (1976) has recently pointed out the usefulness of anamorphs in the taxonomy of sooty moulds, and Martin (1967a,b, 1969a,b,c, 1970) and Jong & Rogers (1972) have used them extensively in studying the Xylariaceae. Further examples abound in the more recent literature.

Anamorphs of the plectomycetes or cleistothecial Ascomycetes, which are often highly developed, have attracted the attention of many taxonomists. Fungi in this group are often easily grown in pure culture, and complete life cycles can be readily observed. Because of this, anamorphs have been used in taxonomy here more than in most other groups.

What is most intriguing in the cleistothecial Ascomycetes is the use of anamorphs to indicate relationships at the family, order, or even class level. Cain (1965a), for example,

suggested that similarities between the anamorphs of the Aspergillaceae (Trichocomaceae) and Hypocreales were evidence of relatedness between these two taxa. Later he used these criteria to help support other proposed relationships.

The moving force behind Cain's proposals of the 1950's was the idea that the cleistothecial Ascomycetes were derived from pyrenomycetous and discomycetous forms. This was a novel idea that was not immediately accepted. In subsequent years, however, Cain and other authors have elaborated on this hypothesis, and it has become more widely accepted. The arguments for Cain's hypothesis are several and have been treated in detail elsewhere. Rather than go through them again here I refer the reader to the series of papers by Cain (1956a, b,c, 1959, 1961a,b,c, 1972), Malloch & Cain (1970a,b, 1971a,b,c,d, 1972a,b, 1973a,b), and Malloch (1970a).

On the following pages I shall be considering the anamorphs of plectomycetes, family by family, to determine whether a taxonomically significant pattern will emerge. The taxonomic scheme to be followed is derived from that of Cain and co-workers. Certain changes in thought have occurred during and after those studies, so that the system used here differs somewhat from its predecessors. It is based on the concept of cleistothecial Ascomycetes as derived from four major groups: 1) the Pleosporales, 2) the Diaporthales or Pyrenomycetes, 3) the Hypocreales, and 4) the Pezizales or Operculate Discomycetes.

THE CONIDIAL FORMS

PLEOSPORALES

Sporormiaceae. This family consists of the ostiolate genera *Sporormia* DeNot. and *Sporormiella* Ell. & Ev., and the cleistothecial genera *Preussia* Fckl., *Pycnidiophora* Clum, and *Westerdykella* Stolk. Conidia are produced by some of the species of all of these genera, and are produced in pycnidial conidiomata. In *Pycnidiophora dispersa* Clum the conidia are produced on short cells that closely resemble the wall cells of the pycnidial locule (Kowalski 1964) and are possibly phialides of the type common in the form genus *Phoma*. Pycnidia in species of *Sporormiella* and in *Westerdykella ornata* Stolk seem to have a similar type of conidiogenesis.

Phaeotrichaceae. Neither *Phaeotrichum* Cain & Barr nor *Trichodelitschia* Munk is known to produce conidia.

Zopfiaceae. The only report of conidia in the Zopfiaceae is that of Marchal (1895), who reported that germinating ascospores of *Marchaliella zopfielloides* Bomm. & Rouss. (=*Testudina terrestris* Bizz.) gave rise to colonies bearing conidiophores and chains of brownish conidia. His illustrations suggest long tapering phialides, but it is impossible to be certain. Both von Arx (1971) and Hawksworth & Booth (1974), however, believe that Marchal had a contaminant and that *Testudina* is a Loculoascomycete lacking conidia. It should be pointed out, though, that cultures of this species have not been studied by these critics.

Eremomycetaceae. *Rhexothecium globosum* Samson & Mouchacca is reported to produce solitary, nearly sessile, holoblastic conidia along the vegetative hyphae (Samson & Mouchacca 1975). *Eremomyces* Malloch & Cain, the only other member of the family, has not been reported to produce conidia, although it has been studied in pure culture (Malloch & Cain 1971b).

Xylariaceae. The papers of Martin and Jong & Rogers cited above, report a considerable variety of anamorphs in this family (form genus *Nodulisporium* Preuss, etc.). All of these, however, are in ostiolate species, and the only cleistothecial member, *Pulveria porrecta* Malloch & Rogerson, does not seem to produce conidia. Most species in this family produce holoblastic conidia on sympodial conidiogenous cells, and it would be expected that cleistocarpous forms would conform to this pattern.

Sordariaceae. Only a few species of cleistothecial Sordariaceae are known to produce conidia. Two species, *Zopfiella pleuropora* Malloch & Cain and *Tripterospora erostrata* (Griff.) Cain, have been reported to produce simple, tapering monophialides (Malloch 1970c, Malloch & Cain 1971d), although Udagawa & Furuya (1974) report *T. erostrata* to produce only holoblastic conidia.

Nearly sessile holoblastic conidia have been demonstrated to occur along the vegetative hyphae of *T. erostrata* (Udagawa & Furuya 1974). *Zopfiella pilifera* (Udagawa & Furuya 1972), *Z. marina* Furuya & Udagawa (Furuya & Udagawa 1975), species of *Diplogelasinospora* Cain (Udagawa & Horie 1972), and *Echinopodospora jamaicensis* Robison (Udagawa, Furuya, & Horie 1973). Larger and more well-defined holoblastic conidia, produced singly at the ends of more elongated conidiogenous cells, are reported for *Z. curvata* (Fckl.) Winter (Udagawa & Horie 1974) and *Z. latipes* (Lundqv.) Malloch & Cain (Lundqvist 1969).

Udagawa & Horie (1972) and Udagawa, Furuya & Horie (1973) report all the known species of *Diplogelasinospora* to produce simple chains of thallic conidia through the break-up of vegetative hyphae.

Chaetomiaceae. According to Malloch & Cain (1973b) there are 25 species of cleistothecial Chaetomiaceae, all assignable to the genus *Thielavia* Zopf. Arx (1975) has studied the same species as Malloch & Cain and assigns them to five genera, of which only one, *Chaetomidium* (Zopf) Sacc., is considered to be a member of the Chaetomiaceae. He places the largest genus, *Thielavia*, in the Sordariaceae.

Members of the genus *Thielavia* were divided by Malloch & Cain into four groups: 1) species with holoblastic conidia, 2) species with enteroblastic conidia (phialoconidia), 3) species with thallic conidia, and 4) species lacking conidia (the largest group).

In the holoblastic group were placed *T. sepedonium* Emmons, *T. novoguineensis* Udagawa & Horie, *T. thermophila* Fergus & Sinden, *T. setosa* Dade, and *T. cephalothecoides* Malloch & Benny. The simplest of these are *T. setosa* and *T. thermophila*, where small, sessile, holoblastic conidia are produced along the length of the vegetative hyphae. In *T. sepedonium* and *T. novoguineensis* the conidia are larger and may be borne in a manner similar to that of *T. setosa*, or they may be borne on elongated and branched conidiogenous cells. Occasionally the conidia are produced in short retrogressive chains of two or three. *T. cephalothecoides* produces relatively large conidia singly or in pairs at the apices of highly branched conidiogenous hyphae arising from long brown conidiophores.

The enteroblastic group so far contains only *T. terrestris* (Apinis) Malloch & Cain. In this species conidia are produced in small wet masses or short chains from narrow phialides. The phialides are borne on simple or sparingly branched hyphae.

The thallic group contains only two species: *T. albomyces* (Cooney & Emerson) Malloch & Cain, and *T. cephalothecoides* Malloch & Benny. The conidia in *T. albomyces* are of a thick-walled chlamydosporic type, and are produced irregularly on the vegetative hyphae. In *T. cephalothecoides* a similar type of chlamydospore occurs, but these are usually inconspicuous compared with the accompanying holoblastic type.

Coniochaetaceae. There are three known genera of Coniochaetaceae: *Coniochaeta* (Sacc.) Mass., *Coniochaetidium* Malloch & Cain, and *Ephemeroascus* van Emden, of which the last two are cleistocarpous. Conidia are rare in *Coniochaetidium*, the only report being of scattered, sessile, holoblastic conidia produced along the vegetative hyphae of *C. ostreum* Malloch & Cain (Malloch & Cain 1971d). *Ephemeroascus verticillatus* van Emden produces verticillate groups of tapering phialides along the vegetative mycelium (Emden 1973) and hyaline ameroconidia that collect on the phialide in wet masses.

Melanosporaceae. The Melanosporaceae consists of the pyrenomycetous genus *Melanospora* Corda, and the cleistothecial genera *Microthecium* Corda and *Rhytidospora* Jeng & Cain. Many species of *Melanospora* and *Microthecium* are characterized by phialoconidia. In *Microthecium* the phialides are nearly sessile, flask-shaped, and are borne along the vegetative hyphae (Udagawa & Cain 1969). Conidia are so far unknown in *Rhytidospora*.

Pseudeurotiaceae. This family, as monographed by Malloch & Cain (1970b), contains nine genera, to which three or four more have been subsequently added. Enteroblastic conidia seem to be the most common situation in this family and are borne on long, tapering phialides scattered along the vegetative hyphae (form genera *Acremonium* Link ex Fr., *Verticillium* Nees ex Wallr.). Conidiogenous structures of this type are reported in *Albertiniella polyporicola* (Jacz.) Malloch & Cain (Udagawa & Horie 1971 (as *Cephalotheca splendens* U. & H.)), *Emericellopsis* van Beyma (Beyma 1940, Cain 1956a (as *Saturnomyces humicola* Cain)), *Hapsidospora* Malloch & Cain (Malloch & Cain 1970b), *Mycoarachis* Malloch & Cain (Malloch & Cain 1970b), *Nigrosabulum* Malloch & Cain (Malloch & Cain 1970b), and *Pseudeurotium zonatum* van Beyma (Malloch & Cain 1970b). Udagawa (1965), however, considers the conidia in *P. zonatum* to be holoblastic. The phialides in *Emericellopsis synnematicola* Mathur & Thirumalachar and *E. salmosynnemata* Grosklags & Swift are united into synnemata according to the describing authors. Gams (1971) illustrates them in penicillate clusters in *E. synnematicola* and solitary in *E. salmosynnemata*.

In *Cryptendoxyla hypophloia* Malloch & Cain the phialide differs from those of the preceding species in having a prolonged collarette containing several conidia in a row (form genus *Chalara* (Corda) Rabenh.). It has been described in detail by Nag Raj & Kendrick (1975).

In *Pseudeurotium ovalis* Stolk and species of *Fragosphaeria* Shear the conidia are holoblastic and borne on short sympodial conidiogenous cells. Those of *Fragosphaeria* species are well illustrated by Chesters (1935) (as *Cephalotheca* spp.) while Udagawa (1965) has treated *Pseudeurotium* species.

Conidia in *Xylogone sphaerospora* von Arx & Nilsson (?= *Mycogala marginata* Crooks) are thallic in origin and are produced by the break-up of vegetative hyphae (Arx & Nilsson 1969, Crooks 1935).

The genus *Myxotrichum* Kunze ex Fr. may be a reduced member of this family. Two species are known to produce chains of thallic conidia from the apex of pigmented conidiophores

(form genus *Oidiodendron* Robak). However, other species are known to have "arthroaleuries" (Orr et al. 1963), a curious type of thallic conidia that form in chains and are separated by dead cells. Conidia of this type are best known in the Onygenaceae (see below) and argue for the placement of *Myxotrichum* in that family.

Endomycetaceae. The 15 genera of Endomycetaceae recognized by Redhead & Malloch (1977) range from perithecial to cleistothecial to yeast-like, and exhibit a bewildering array of anamorphs. Upadhyay & Kendrick (1975) have studied the ostiolate genera *Ceratocystis* Ell. & Halst. and *Ceratocystiopsis* Upadhyay & Kendrick, and have described holoblastic and enteroblastic developmental types encompassing 16 form genera.

In *Ceratocystis*, the more complex of the above two genera, the holoblastic anamorphs can be subdivided into: 1) those forming acropetal chains of conidia, 2) those with annellides, and 3) those with sympodial conidiogenous cells. In the sympodial type there is a basic simple structure (form genera *Sporothrix* Hektoen & Perkins, *Hyalorhinocladiella* Upadhyay & Kendrick), a penicillate mononematous form (form genus *Verticicladiella* Hughes); and two synnematous forms (form genera *Pesotum* Crane & Schoknecht, *Hyalopesotum* Upadhyay & Kendrick).

The annellidic type apparently has not been seen in the simple form, but is known in both the penicillate-mononematous (form genus *Leptographium* Lagerb. & Melin) and synnematous (form genera *Graphium* Corda, *Graphilbum* Upadhyay & Kendrick) forms.

The phialidic type is known from the simple (*Acremonium* Link ex Fr., *Chalara* (Corda) Rabenh.), the penicillate-mononematous (form genus *Phialocephala* Kendrick), and synnematous (form genus *Phialographium* Upadhyay & Kendrick) forms.

In *Europhium* Parker, a cleistothecial form, the conidia are borne on either of two types of conidiogenous structures. According to Davidson & Robinson-Jeffrey (1965), *E. trinacriforme* Parker produces its conidia on penicillate-mononematous structures bearing annellides (form genus *Leptographium*), and those of the other three species are produced on similar structures bearing sympodial conidiogenous cells (form genus *Verticicladiella*). Upadhyay & Kendrick (1975), it should be pointed out, consider *Europhium* to be synonymous with *Ceratocystis*.

It should also be noted that von Arx (Chap. 13) restricts the genus *Ceratocystis* to those species with anamorphs in the form genus *Chalara*, disposing all other species formerly assigned to *Ceratocystis* in the genus *Ophiostoma*.

Amorphotheca Parbery is a genus characterized by ascomata with amorphous and non-cellular walls. Anamorphs in this group produce holoblastic conidia in acropetal chains. Arx (1973b) has illustrated this kind of anamorph, and assigned it to the form genus *Hormoconis* von Arx & de Vries. Arx (1973b) also considered the conidia of *Ambrosiozyma* van der Walt to be of this type. Hyaline or pale anamorphs referable to the form genus *Hyalodendron* Diddens occur in *Ceratocystis* and *Endomyces* Reess (Upadhyay & Kendrick 1975, Redhead & Malloch 1977).

Arx (1973b) included in the genus *Endomyces* forms with simple thallic conidia of the *Geotrichum* type; but this type of development was excluded from the Endomycetaceae by Redhead & Malloch (1977), who transferred such species to the Schizosaccharomycetaceae and Onygenaceae.

Microascaceae. The Microascaceae contains five genera, according to Malloch (1970a), of which three are ostiolate and two cleistothecial. An additional ostiolate genus, *Pithoascus* von Arx, was proposed by Arx (1973a).

Most species of Microascaceae produce blastic conidia on annellidic conidiogenous cells. In the majority of species of *Microascus* Zukal, an ostiolate member of the family, the annellides are produced on complex penicillate structures (form genus *Scopulariopsis* Bain.). In species of *Petriella* Curzi, the same type of anamorph may exist, but the conidiophores may also be borne in synnemata (form genus *Graphium*). *Scopulariopsis* and *Graphium* anamorphs characterize the plectomycetous genus *Kernia* Nieuwland, while *Petriellidium* Malloch has species provided with annellides only in the synnematous condition.

Holoblastic conidia produced on sympodial conidiogenous cells are also common in the Microascaceae, and are usually simple structures (form genera *Sporothrix*, *'Scedosporium'*). *Microascus giganteus* Malloch differs from other members of the family in producing large, dark, holoblastic conidia either terminally or sympodially on simple to penicillate conidiophores (form genus *Wardomyces* Brooks & Hansford).

Species of *Lophotrichus* R.K. Benj. and *Pithoascus* von Arx lack conidia, or at most produce a few chlamydospores on the substrate hyphae.

Cephalothecaceae. *Cephalotheca sulfurea* Fckl. is the only species now maintained in this family. Conidia are reported by Chesters (1935) to be borne on phialides that are produced singly or in small clusters at the apex of short conidiophores (form genus *Paecilomyces*).

HYPOCREALES

Nectriaceae. The complex phialidic anamorphs known in this family also characterize the cleistothecial species *Roumegueriella rufula* (Berk.& Br.) Malloch & Cain. In this species a penicillus of phialides produces wet masses of conidia in small heads (form genus *Gliocladium* Corda).

Heleococcum japonense Tubaki is characterized by a simpler anamorph producing conidia in small masses at the apex of a long, tapering conidiogenous cell. Tubaki (1967) described the conidia as being produced in the manner of the form genus *Trichothecium* Link, where each successive conidium is produced as the blown out end of the conidiophore. My own observations suggest that they may be phialides.

Species of *Sphaeronaemella* Karst. produce long, tapering phialides on sparingly to richly branched conidiophores closely resembling those of the pyrenomycetous genus *Nectria* Fr. Samson & Gams (Samson 1974) described the form genus *Gabarnaudia* for these structures.

Trichocomaceae. The Trichocomaceae, *sensu* Malloch & Cain (1972b) now includes 20 genera. Conidia in this family are nearly always borne on complex phialidic structures. Most members of the family have anamorphs referable to the form genera *Aspergillus* Mich. ex Fr. or *Penicillium* Link ex Fr. and, as such, have been studied in detail by Raper & Fennell (1965) and Raper & Thom (1949). More recently Stolk & Samson (1972), Stolk & Scott (1967), Stolk (1968), Scott & Stolk (1967), and Scott (1968a,b) have reexamined the genera with *Penicillium* anamorphs.

Aside from anamorphs of the *Penicillium* and *Aspergillus* type, a few species produce less complex structures; some referable to *Paecilomyces* or *Polypaecilum* G. Smith.

Ascobolaceae. The only cleistocarpous species of this family, *Guilliermondia saccoboloides* Boud., is not known to produce conidia.

Monascaceae. Species of *Monascus* are characterized by holoblastic conidia produced in basipetal chains from retrogressive conidiogenous cells. This anamorph was studied by Cole & Kendrick (1968) and assigned to the form genus *Basipetospora* Cole & Kendrick.

Onygenaceae. When the Onygenaceae was treated by Malloch & Cain (1971a), seven genera were recognized. I now include with this group the species usually placed in the Gymnascaceae which, along with a few recent additions, brings the number of genera to 30.

Probably the most characteristic feature of the conidia in this family is that they are never enteroblastic. Many species produce holoblastic conidia, although these anamorphs have not evolved to the level of complexity found in certain other families. They usually produce solitary lateral or terminal conidia directly along the vegetative hyphae or on conidiophores of varying complexity. Form genera to which some of these fungi are ascribed are: *Chrysosporium* Corda, *Microsporum* Gruby, *Trichophyton* Malmsten, and *Histoplasma* Darling.

Thallic conidia are also produced; often by the simple break-up of chains of cells on the vegetative hyphae (form genus *Geotrichum* Link). In addition, a characteristic type of swollen, catenulate, thallic conidia alternating with dead or empty cells (form genera *Malbranchea* Sacc., *Geomyces* Traaen) also occurs. Conidia of this type are called "arthroaleuries" by Orr et al. (1963), and "alternate arthroconidia" by Sigler & Carmichael (1976). The taxonomy of form genera characterized by such conidial structures is very thoroughly treated by Sigler & Carmichael (1976).

The genus *Myxotrichum* (discussed under the Pseudeurotiaceae) is unlike all other Onygenaceae in having very darkly pigmented ascomata. Because of this I have reservations about treating it with the Onygenaceae, although the presence of well-developed thallic conidia most strongly suggests this family. Perhaps the best solution would be to put *Myxotrichum* and the closely related genera *Toxotrichum* Orr & Kuehn, *Tripedotrichum* Orr & Kuehn, and *Byssoascus* von Arx into a separate family.

Pyronemataceae. The cleistothecial species of the Pyronemataceae do not usually produce conidia. The only two species known to do so are *Xeromyces bisporus* Fraser and *Cleistothelebolus nipigonensis* Malloch & Cain.

In *X. bisporus*, conidia are produced holoblastically. They may be one- to several-celled, and occur as swollen end cells of the vegetative hyphae.

Conidia of *C. nipigonensis* are possibly also holoblastic, but are produced successively from inconspicuous loci along the vegetative hyphae in a manner suggestive of the form genus *Hormonema* Lagerb. & Melin. Liquid cultures of this species produce yeast-like budding cells and few hyphae (Malloch & Cain 1971b).

DISCUSSION

From the preceding section I think it is apparent that there are two kinds of taxa containing cleistothecial members: those characterized by abundant conidium production, and those in which conidia are absent, or at least not conspicuous throughout. From a taxonomic point of

view this is interesting, because the fungi in the first group are members of purely cleistothecial or further reduced families without obvious phylogenetic connections to ostiolate or apothecial groups, while those in the second category are usually members of predominatly pyrenomycetous or discomycetous families.

From the above observation I am led to conclude that in the highly evolved and complex families Endomycetaceae, Microascaceae, Onygenaceae, Pseudeurotiaceae, and Trichocomaceae, anamorphs have undergone a particularly rich evolution. The main reason for this may be that *once forcible discharge is lost, conidia share dispersal mechanisms with ascospores.* In the highly specialized habitats most of these fungi occupy, the number of possible dispersal agents would be limited, and the fungi might well concentrate all their resources on one of them. A second possibility is that passive spore dispersal is likely to be more random and to require much greater numbers of spores.

The Endomycetaceae are perhaps the richest in anamorphs, and in this respect bear little resemblance to any group of conventional Ascomycetes. It seems reasonable to assume that if these fungi are derived from a pyrenomycetous group, their ancestors had, at least to a limited extent, the structures from which elaborate anamorphs could evolve. I am inclined to believe that the basis for this evolution was the versatile and ever-present phialide.

If we assume that the ancestor of the family had a simple phialide similar to the present *Acremonium* or *Chalara* type, it is not difficult to imagine the evolution of penicillate mononematous and synnematous structures. These structures duplicate the morphology and ecology of the ascoma of *Ceratocystis* and undoubtedly evolved parallel to it. This is in accordance with the hypothesis that, in this and other advanced families, conidia tend to be dispersed by the same mechanisms as ascospores.

It does not seem likely that the annellidic and sympodial holoblastic types would have had separate ancestors. It is more reasonable to visualize the phialide becoming simplified to yield these two types. The step from a phialide to an annellide is a very short one, involving only minor changes in the time required for conidium wall solidification. Reduction of a phialide to a sympodial holoblastic type is somewhat more complex. Instead of the phialoconidia becoming modified, it is more likely that the whole phialide would become the conidium. The phialides borne in clusters at the apex of a conidiophore (as in *Penicillium*) are, in fact, already holoblastic and developed from a sympodially proliferating axis.

Gams (1973) presented several examples of species in which solitary conidia are apparently produced on phialides. Such conidia seem to be holoblastic, as are the first-formed conidia of a phialide. In Gams' example, particularly in a comparison of a phialidic species of *Lasiosphaeria* with one having holoblastic sympodial conidia, it would appear that the tip of the phialide itself may become sympodially proliferated.

The catenulate holoblastic conidia in the Endomycetaceae may have their origin in a phialide where the initial conidium remains in place and produces a holoblastic bud at its apex. Such a process might be repeated to produce a chain. On the other hand, these forms seem sufficiently different from the other holoblastic forms to suggest an independent origin.

In the Microascaceae, phialides appear to be lacking, and to be replaced by annellides. Again, I propose a phialidic ancestor for this family. The sympodial and non-proliferating holoblastic anamorphs in the Microascaceae probably followed the same pattern of evolution as

those of the Endomycetaceae. The form genus *Wardomyces*, for example, is remarkably similar to certain forms of *Scopulariopsis*. In *Microascus giganteus* the conidiophores are penicillately branched and bear the conidia at the apex of annellide-shaped conidiogenous cells. The conidia with germ slits in *M. giganteus* are larger but similar to the annelloconidia of *M. singularis* (Sacc.) Malloch & Cain. Some species (ascomata still unknown) produce both annellidic and nonproliferating forms on the same colony (Gams 1968, Malloch 1970). In some species of *Petriella*, both sympodial and annellidic forms can occur together.

Anamorphs in the Pseudeurotiaceae are simpler than those of the previous two families. The basic type is again the phialide, and these may aggregate to form fairly complex, penicillate, mononematous or synnematous structures in *Emericellopsis*. Annellides are absent, but there has been some tendency toward sympodial holoblastic conidia in the genera *Fragosphaeria* and *Pseudeurotium*.

Familiar to all mycologists, of course, are the complex phialidic forms of the Trichocomaceae. In this family there does not appear to have been a development of other conidium types, as occurred in the Endomycetaceae and Microascaceae. Instead, the phialidic form has undergone a considerable evolution. Malloch & Cain (1972b) suggest a hypothetical ancestor for the Trichocomaceae resembling the hypocreacean genus *Hypocrea* Fr. During the evolution of the Trichocomaceae, Malloch & Cain believe that there was a progressive loss of stromatic and ascomatal tissues, resulting in the present species that range in complexity from ascomata borne several in a stroma (*Petromyces* Malloch & Cain) to naked clusters of asci (*Edyuillia* Subr.).

Malloch & Cain described a general reduction and consolidation of conidium-bearing structures, that they believed to occur parallel to ascoma reduction. The most primitive form would have terminal clusters of phialides borne at the apices of loosely spreading branches of the conidiophore (form genus *Paecilomyces)*. From this type, reduction would be toward greater compactness, ending in a tight cluster of phialides on a swollen conidiophore apex (form genus *Penicillium*). The *Aspergillus* line of anamorphs demonstrates this particularly well, ranging from the almost branched structures in *Emericella* Berk. & Br., to the radiating system of metulae and phialides in *Petromyces*, to the compact cluster of phialides on a radiating head in *Eurotium*.

The Onygenaceae differ from the families just discussed in lacking phialides and their derivatives. Cain (1959) proposed a pezizalean ancestry for this group, and supported his arguments with the fact that phialides are lacking in both groups.

Although under the apparent handicap of lacking phialides, the Onygenaceae have produced a considerable development of conidial structures. In this family, holoblastic conidiogenesis from non-proliferating loci, and thallic conidia, are developed to a greater degree than in any other group of fungi. The only similar development is to be found in the Agaricales, where phialides are also lacking. Although "arthroaleuries" (alternate arthroconidia) are particularly characteristic of the Onygenaceae, Orr et al. (1977) do not consider them to be of taxonomic significance above the species level.

In the rest of the families containing plectomycetous forms, conidium development has not evolved beyond the level found in their ostiolate or apothecial relatives. Conidia are certainly conspicuous in some of these groups, but only serve to underline obvious relationships.

The only exception to this is perhaps in the genus *Monascus;* but it may well represent the sole genus in a highly evolved family, and not just a simple, reduced discomycete.

To summarize, I offer the following conclusions:

1. In less highly evolved families of cleistothecial fungi, anamorphs are not highly developed, and closely resemble those of apothecial or perithecial ancestral forms.
2. The families Endomycetaceae, Microascaceae, Onygenaceae, Pseudeurotiaceae, and Trichocomaceae are highly evolved plectomycetous families showing considerable richness in anamorphs.
3. Conidial dispersal mechanisms come to resemble those of the ascospores in highly evolved ascomycetes lacking forcible spore discharge.
4. In the highly evolved families of plectomycetous species with phialidic ancestors, there is an evolutionary trend from simple phialides to annellides to sympodial holoblastic forms.
5. In the Trichocomaceae, evolution of anamorphs has proceeded from loose branching to compact swollen vesicles bearing phialides.

DIALOGUE FOLLOWING DR. MALLOCH'S PAPER

MALLOCH: In several groups we find that there are phialidic, annellidic and sympodial anamorphs share common conidiophore morphology. This is particularly true in *Ceratocystis,* which has *Phialocephala, Leptographium* and *Verticicladiella* anamorphs. I believe that these have not evolved separately, but that one has given rise to the other two, and that Dr. Madelin's hypothesis would explain beautifully how this happened. The taxonomy of both anamorph and teleomorph backs this up very well. All three anamorphic genera are almost identical except for the point at the tip of the conidiogenous cell at which conidia are produced. And the species of *Ceratocystis* involved are certainly morphologically and ecologically similar -- they are obviously related.

KENDRICK: When I worked in Ottawa, there was a sort of dogma that ran: one conidiophore has one kind of conidiogenesis. But as I looked at more and more *Ceratocystis* anamorphs, I began to worry, because I thought some of them were doing more than one thing -- and now I'm quite convinced that some of them do exhibit more than one kind of conidiogenesis on a single conidiophore, either concurrently or sequentially. I believe Dr. Madelin has given us a truly insightful explanation of how these seeming anomalies occur. Mrs. Wang has shown us several examples of anamorphs which produce more than one kind of conidium on neighbouring cells. This kind of thing has been circulating in the mycological underground for some time, and I think it is time for it to be brought out in the open. It may dispel some of our long-cherished hopes, but this kind of awakening is essential if mycological thought is to progress.

VON ARX: In many of the thermophilic fungi, for example *Thielavia* and *Pseudeurotium,* it is often difficult to decide whether the conidiogenous cells are phialidic or sympodial. In the same species it may sometimes be phialidic and sometimes sympodial.

DE HOOG: In some groups, the conidiogenous cell starts life in the annellidic mode, then changes to the sympodial mode. But I've never seen it happen the other way round.

MALLOCH: All this means that in some cases there is not too much taxonomic value in the conidiogenous cell itself, but a lot of useful taxonomic information in the structures that bear conidiogenous cells -- the complex conidiophores of the *Verticicladiella - Phialocephala - Leptographium* group, for example.

DE HOOG: But if you grow these fungi in culture, they soon cease producing such characteristic structures, and form less and less well-organized conidiophores: they degenerate, and almost merge with anamorphic genera of simpler form. So it isn't just the conidiogenesis that can change. The conidiophore is also mutable. Next to a *Pesotum* synnema there will be single *Sporothrix* conidiophores: the longer it is grown in culture, the more the balance shifts toward the *Sporothrix* and away from the *Pesotum* type of fructification.

DICOSMO: We have noted anamorphs for *Aphanoascus* in *Paecilomyces* and in *Chrysosporium*. Where does *Aphanoascus* belong?

MALLOCH: Zukal's original concept of this genus was rather different from Udagawa and Takada's recent (1973) neotypification. Zukal described a *Chrysosporium* anamorph. Udagawa thought that this anamorph was not really part of the fungus, and ignored it. So I believe he has designated as neotype something that does not represent Zukal's material. Udagawa's fungus produced a *Paecilomyces* anamorph. To me, *Aphanoascus* is synonymous with *Anixiopsis*, it has a *Chrysosporium* anamorph, and belongs in the Onygenaceae. Udagawa's material belongs to an undescribed genus of Trichocomaceae.

VON ARX: I'd prefer to maintain *Aphanoascus* sensu Udagawa. Zukal's taxon is based only on some drawings, and as we know, he often mixed things up, producing taxa composed of discordant elements. At least with Udagawa's concept, we have a neotype to examine if necessary.

MALLOCH: Zukal's drawings were good. In addition, Dangeard later found what appeared to be the same thing, and did a very detailed developmental study on it. I don't have too much trouble with this generic concept. But it could, I suppose, be one of many points of contention in these fungi. [The discussion then turned to ecological matters, and Dr. Malloch continued as follows:]

Sphaeronaemella helvellae is a common parasite of two species of *Helvella infula* in northern regions. The necks of the *Sphaeronaemella* ascomata stick out of the *Helvella* hymenium like bristles, and exude ascospores into a slimy droplet. The *Gabarnaudia* anamorph protrudes just as far, and produces a slimy mass of conidia. The parasite occurs on only two species of *Helvella* which are not especially common, so there is a problem of locating new hosts. If an insect vector visits fleshy fungi at random it will pick up spores of the *Sphaeronaemella* and waste them on non-host macrofungi. I suggest, therefore, that there is a specific arthropod vector that visits only *Helvella infula* and closely related species. That seems the only reasonable explanation for the success of the parasite.

WATLING: We should not be surprised by this kind of thing. There are many groups of host-specific insects. Buxton (1960), Edwards (1913, 1925, 1933) and Joy (1932) have produced good accounts of the Mycetophilidae and various other insects, tabulating insects vs.

fungi. Certain flies and beetles visit or inhabit only certain groups of fungal species.

MALLOCH: It is interesting to catch these insects and let them walk around on an agar plate. We have done this with dung-inhabiting animals, and found that we recovered many of the slimy-spored coprophilous fungi. This would be an interesting field of fungal ecology for someone to explore.

MADELIN: Where fungi are exposed to the stress of changing seasons I can understand why they need both anamorph and teleomorph developing at different times and serving rather different purposes, such as dispersal and survival. But many of the cleistothecial forms appear to inhabit protected sites -- soil, compost, silage, inside bark -- and one wonders why the fungus still produces both forms, especially when, as you have just told us, they appear to be more or less equivalent in stature and dispersal method. Not only that, the two forms are produced side by side, simultaneously. Can anyone suggest why?

MALLOCH: I think you have correctly diagnosed the situation, and I believe that if we look at the broad picture, there is a tendency for these fungi to lose the teleomorph. This is probably why so many species of *Penicillium* and *Aspergillus* have not been connected with a teleomorph. They evolved a new mechanism for genetic recombination -- parasexuality -- and then simply stayed with the simpler, less energy-consuming anamorph.

KENDRICK: Even if the teleomorph is not entirely selected against, it is often much the rarer of the two forms. If you look at samples of Dutch elm disease, you'll find the *Pesotum* anamorph a hundred times for every time you see the ascomata of the teleomorph.

WEBSTER: This may be because the fungus is heterothallic, and opportunities for mating may arise infrequently.

MALLOCH: Oddly enough, the Trichocomaceae are seldom heterothallic. That is probably true in the Microascaceae as well. But many Onygenaceae are heterothallic.

WEBSTER: That may be due to a kind of selection process: you are less likely to see the teleomorph of a heterothallic species than of a homothallic one.

LUTTRELL: If a fungus retains both teleomorph and anamorph, it may be capable of responding to a wider range of environmental conditions. But the production of an abundance of spores of two kinds may well indicate that the organism is very inefficient. Perhaps I can use the example of *Apiosporina morbosa* again: it gets two shots at the same substrate in successive years. But if you consider infections that started in successive years, then you will have ascospores and conidia being produced at exactly the same time, although on different galls of different ages. Perhaps this gives the fungus more flexibility, and if conditions are unsuitable for the production of conidia on one gall, they may still permit the liberation of ascospores from another. You might think that such a fungus must be a very efficient pathogen, but this is not so. Despite its production of two kinds of spores, it can hardly move out of the canopy of one tree onto the next. One tree may be covered with galls, the next be totally unaffected. The fungus must produce so many spores simply because it is so inefficient.

MALLOCH: In the case of the Trichocomaceae we may be misled by what we see in a petri dish culture. On the natural substrate you may find just a few cleistothecia and one or two conidiophores.

WERESUB: What is the nature of the sclerotia that so often occur in Trichocomaceae?

MALLOCH: I think these are stromata that have yet to be persuaded to complete their life cycle. They are particularly common in *Penicillium* -- for example *Penicillium thomii*. Ultimately we should be able to induce them to go all the way and produce the teleomorph.

The next chapter focusses more narrowly on a much-studied group of related Ascomycete genera and their diversified phialidic anamorphs. Among other things, the authors discuss possible evolutionary trends in these anamorphs, and the implications for the taxonomy of the holomorphs.....

11
Conidia and Classification of the Nectrioid Fungi

G.J. Samuels & A.Y. Rossman

The three basic genera of the Hypocreales are *Hypomyces* (Fries) L.-R. Tulasne, *Hypocrea* Fries and *Nectria* Fries, around each of which are clustered a variety of derived genera. This paper discusses the largest and most economically important of these basic genera, *Nectria*, and its better known segregates, referred to here as the nectrioid fungi.

Nectria includes pyrenomycetous species having non-immersed, brightly coloured perithecia and hyaline, non-apiculate, one-septate (didmyosporous) ascospores, the cells of which do not separate at the septum. Over 300 species have been proposed for the genus. Fries' original description of the genus did not restrict it to species with didymosporous ascospores but Saccardo (1878,1883) gave an amended description limiting *Nectria* to species with one-septate ascospores. Saccardo and others (Seaver 1909a,b, Petch 1938, to mention just a few) proposed generic names for almost every possible variant of the original description. There resulted genera based on such single characters as ascospore septation, colour or ornamentation; relationship of the perithecium to the substrate or to a stroma or subiculum; perithecium colour or ornamentation; and the conidial phase (anamorph). Most of these characters, such as perithecium ornamentation or stroma formation, are either too variable to be taxonomically valuable, or are too broad, when used alone, to delimit natural genera.

Weese (1912, 1914a,b, 1916, 1918, 1919 and others), Höhnel's student, observed that perithecium wall structure in the nectrioid fungi is not widely variable within a species. He found that groups of species having a similar perithecium wall structure also shared features of perithecium ornamentation, stroma, ascospore form, structure of the ascus apex, and habitat. He also demonstrated that features previously used as generic determinants, such as stroma formation, have arisen many times and in species that are not otherwise closely related. It is unfortunate that Weese never published a monograph: nevertheless his work has had a profound influence on later mycologists.

Wollenweber (1913, 1926) emphasized conidial form rather than perithecial form in his studies. He (1926) divided *Nectria* into four sub-genera and several sections and subsections on the basis of features of the anamorphs like conidium septation and conidiomata. Although Wollenweber did not expressly use perithecium morphology in his scheme, his subsections could be defined on the basis of perithecium wall structure, thus demonstrating the close correlation between sexual and asexual morphology.

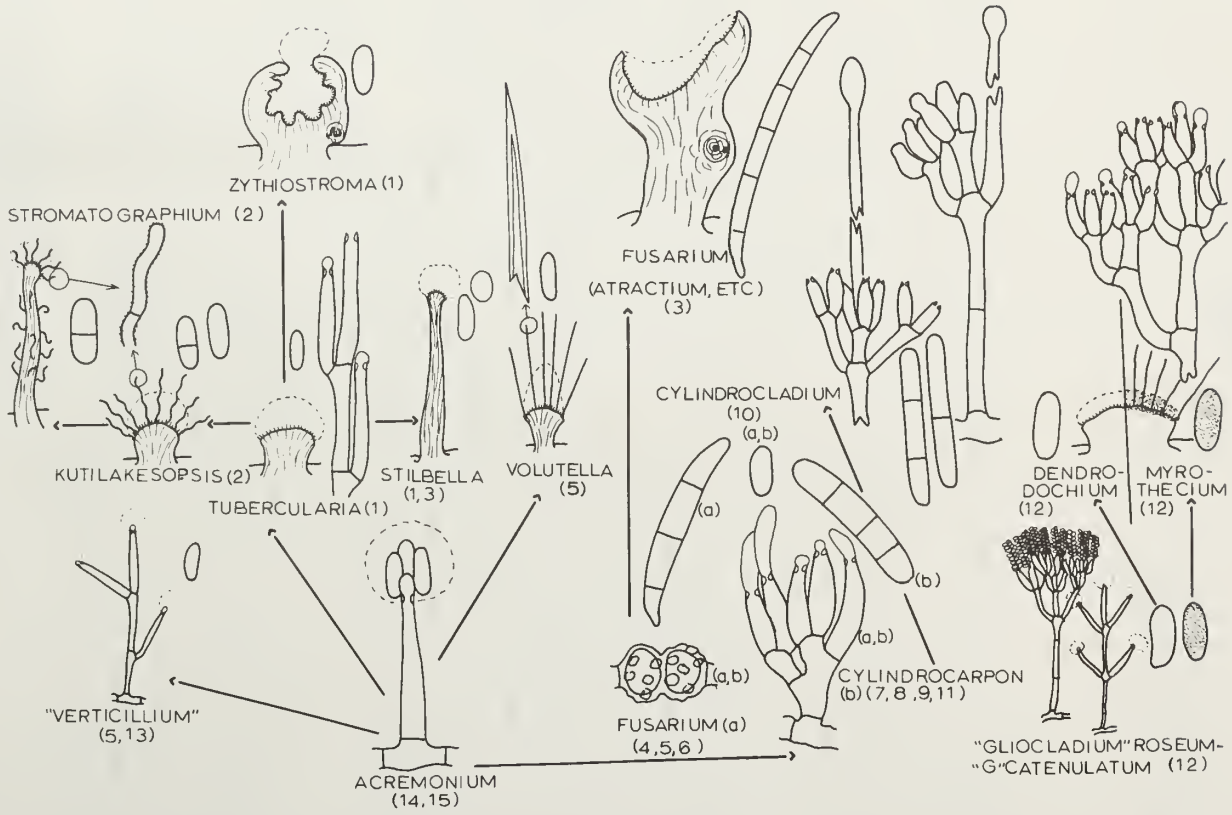

Fig. 11.1 The major types of anamorph found among the nectrioid fungi Numbers in parentheses refer to the perithecial types shown in Fig. 2. Arrows indicate possible lines of derivation.

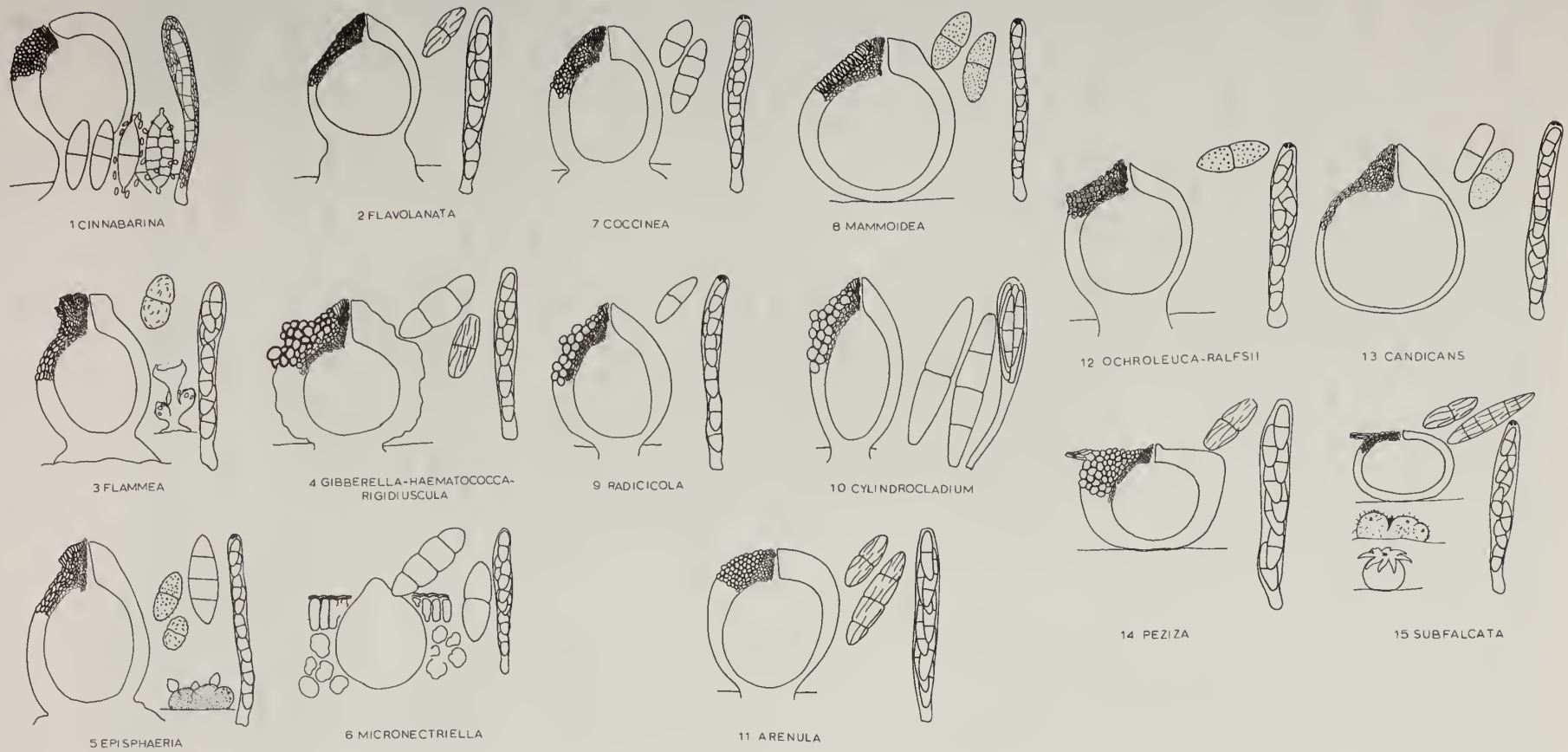

Fig. 11.2 Fifteen basic types of perithecia found in the nectrioid fungi. The range in ascospore form and septation is shown.

Through the work of Weese and Wollenweber, taxonomy of the nectrioid fungi has progressed a long way from the artificial saccardoan system, as is reflected in monographs by Dingley (1951), Booth (1959, 1966, 1971) and Samuels (1976a). However, 'The Curse Of The Single Character' is still with us. Closely related species are still placed in different genera because of differing numbers and arrangements of ascospore septa. Wollenweber (1926) and Booth (1959, 1971) recognized the relationship between species of genera having didymosporous, phragmosporous, scolecosporous and dictyosporous ascospores. Booth (1959) divided *Nectria* into groups of species on the basis of perithecium wall structure and anamorph, and included non-didymosporous species in the groups, but both he and Wollenweber retained the old generic concepts dictated by ascospore septation. Consequently we are left with an artificial system wherein most genera are defined on the single character of ascospore septation (see review in Rogerson 1970).

Fungi Imperfecti bear the same burden of artificiality that is found in the nectrioid fungi. By definition, form-genera of Fungi Imperfecti are based purely on morphological grounds, making it difficult to recognize relationships between species or genera. Research elucidating conidium ontogeny has advanced our understanding of conidial fungi into an area of rational study. But even with an understanding of developmental differences we are left with large, ontogenetically similar groups within which one cannot define natural genera. Anamorphs of nectrioid fungi represent only one among many groups of phialidic fungi (Fig. 11.1).

In the following pages an outline of morphological variation in the nectrioid fungi is presented, showing that anamorphs are instrumental in defining natural groups of Ascomycetes, and conversely, that teleomorphs can indicate natural groups of Fungi Imperfecti. We believe that knowledge of variation in the nectrioid fungi can give useful clues for study and reclassification of other, less well known groups of Ascomycetes. Details of perithecium structure are given in the cited references and in Fig. 11.2.

I. GENERAL CHARACTERISTICS

In culture, colonies are light-coloured or brightly-coloured, never dark. Phialides are borne on conidiophores which may be scattered, or united into sporodochial, synnematal or pycnidial conidiomata. Three types of conidia occur in this group: blastic-phialidic amerospores, blastic-phialidic phragmospores, and chlamydospores. The three forms may occur in any combination or singly, with the exception of chlamydospores which are never found alone in healthy isolates.

II. AMEROCONIDIAL ANAMORPHS WITH SOLITARY CONIDIOPHORES

The genera represented under this heading are *Acremonium* Link ex Fries, *Verticillium* Nees ex Wallr., and *Gliocladium* Corda.

Acremonium is characterized by an unbranched or infrequently branched conidiophore bearing a solitary phialide which produces hyaline, unicellular conidia. The tip of the phialide is unflared, the walls of the conidiophore are unthickened, and colonies are light-coloured. The genus was monographed by Gams (1971).

This simple *Acremonium* morphology is often encountered in the fungi. *Acremonium* states include anamorphs of the hypocreaceous but non-nectrioid genera *Hypocrea* and *Hypomyces*. Many nectrioid fungi having aggregated conidiophores in nature may produce only *Acremonium*-like phases in pure culture, and species of *Fusarium* Link ex Fries and *Cylindrocarpon* Wollenweber often have *Acremonium*-like microconidial states. Any one of the *Acremonium*-like anamorphs, taken by itself, could be placed in *Acremonium*, but our knowledge of the sexual states (teleomorphs) makes it clear that their actual affinities are diverse.

Two groups of *Nectria* are known to have *Acremonium* sensu stricto as their anamorphs; the *N. peziza* (Tode ex Fries) Fries-group (Booth 1959, Samuels 1976a,b), and the *N. subfalcata* Hennings-group (Samuels 1976a,b). Anamorphs of the two groups can be distinguished; but the distinction, because it is so fine, is not useful in a taxonomic treatment. Conidiophores of the *N. peziza*-group tend to have thinner walls and to be slightly wider at the base relative to the tip than those of the *N. subfalcata*-group. Conidium production in culture is usually poor for the *N. peziza*-group, but usually prolific in the *N. subfalcata*-group.

Nectria peziza and its relatives could be retained in their own genus. Because of their thick perithecium wall and collabent aspect, the species are easily placed within a series of their own. Munk (1957) proposed the genus *Neuronectria* for *Nectria peziza* because of its striate ascospores. Although species in the *N. peziza*-group do tend to have striate ascospores, this feature is also found in various other nectrioid fungi. The only known anamorph for the group is *Acremonium*. As far as is known, species of the *N. peziza*-group possess only didymosporous ascospores.

Of the more than ten species now included in the *N. subfalcata*-group, two have multiseptate ascospores. The only known anamorphs are of the *Acremonium* type, with the exception of *N. corynospora* Samuels, which has a *Cylindrocarpon*-like anamorph (Samuels 1978). *Nectria macrostoma* (Berk. & Curt.) Höhn. has been placed in *Sphaerostilbe* L.-R. Tul. & C. Tul., and *Stilbocrea* Patouillard, because of its synnematous anamorph. Other species in the group have been placed in *Neohenningsia* Koorders, *Actiniopsis* Koorders and *Peristomialis* Starbäck, genera described for their hirtose perithecia. Samuels (1976b) placed *Noehenningsia* and *Peristomialis* in synonymy with *Nectria*, and Santesson (1952) found that *Actiniopsis* was a genus of non-hypocrealean, lichenized fungi.

Acremonium, in its restricted sense, cannot have branched conidiophores, but this is an impractical distinction because branches may arise on some conidiophores of any isolate. The problem arises in determining when *Acremonium* has become *Verticillium*. *Verticillium* in its classic sense, consisting of long, erect conidiophores having evenly spaced whorls of phialides, is not found in the nectrioid fungi, but is the anamorph of *Hypocrea* spp., *Hypomyces* spp. (in association with *Sepedonium* aleuriospores) and of species of the clavicipitaceous genera *Cordyceps* (Fr.) Link and *Torrubiella* Boud. Unfortunately there are many nectriaceous anamorphs that cannot be tidily filed in either *Acremonium* or *Verticillium*, because most, but not all, of their conidiophores are branched, but do not form well-developed whorls of phialides.

At least two groups of nectriaceous fungi have this type of anamorph. The anamorphs of *N. candicans* (Plowr.) Samuels (Samuels 1973) and its relatives are white. The species of this

group are found on Myxomycetes and are homogeneous in perithecium structure and anamorph. Members of the group have been placed in *Hyphonectria* (Sacc.) Petch, *Nectriopsis* Maire and *Hypomyces*, genera characterized by having perithecia embedded in a subiculum. Most of the species also have perithecial hairs which could place them in *Lasionectria* (Sacc.) Cke. All the known species have didymosporous ascospores.

A group closely related to the *N. candicans*-group in perithecium structure is the *N. leucorrhodina* (Mont.) Samuels-group (Samuels 1976a). These species are found as hyperparasites on meliolaceous leaf parasites. Repeated attempts by us to grow members of the group in culture have failed, and there do not appear to be any constantly associated anamorphs in nature. Gams (1971) recorded a branching *Acremonium* anamorph for *Calonectria cephalosporii* Hansf. [= *Nectria leucorrhodina* (Mont.) Samuels].

A problematical *Acremonium-Verticillium*-like anamorph similar to that of the *N. candicans*-group is also found for *N. vilior* Starb. and *N. cosmariospora* Ces. & de. Not., closely related species occurring on other Ascomycetes. Their anamorphs are green *Verticillium*-like fungi. Perithecium morphology places these species in the *N. episphaeria* (Tode ex Fr.) Fr.-group (Booth 1959), which is partially characterized by anamorphs in *Fusarium* sect. *Episphaeria* Booth, and by a fungicolous habit.

Some non-hypocreaceous anamorphs are superficially similar to *Acremonium*. The form-genus *Monocillium* Saksena has a simple phialide with a thin-walled, swollen apex and a thick-walled base; cultural characteristics are like those of *Acremonium*. The teleomorph of *Monocillium* is the black, sphaeriaceous genus *Niesslia* Auersw. (Gams 1971). Phialides of some *Niesslia* anamorphs lack a swollen apex, but have a thick-walled base. If this wall-thickening were overlooked, these isolates would be identified as *Acremonium*.

Acremonium also merges with *Phialophora* Medlar. *Phialophora*, more heterogeneous than *Acremonium*, is characterized by grey to black colonies producing simple conidiophores bearing one to several phialides with a well-defined, often swollen venter, an often cupulate or flaring collarette, and amerosporous conidia (Cole & Kendrick 1973). Although this appears to be a well defined genus, some species illustrated by Cole & Kendrick and by Schol-Schwarz (1970) have poorly defined collarettes and some have light, often salmon-coloured colonies (e.g., the *Phialophora hoffmannii*-group of Schol-Schwarz). The distinction between the form-genera *Phialophora* and *Acremonium* is thus not unequivocal.

Known teleomorphs of *Phialophora* are found in many groups of Ascomycetes, including Discomycetes, Pyrenomycetes and Loculoascomycetes. Some of the light coloured *Phialophora* spp. are anamorphs of Discomycetes, but others belong to various species of the pyrenomycetous genus *Coniochaeta* (Sacc.) Massee. Like *Acremonium*, *Phialophora* represents a basic type of anamorph (Gams & Holubová-Jechova 1976). Variations of its structure lead to genera such as *Margarinomyces* Laxa, *Codinaea* Maire, *Menispora* Pers. ex Chev., *Chalara* (Cda.) Rabenh., *Chloridium* Link, and others. An understanding of the relationships of these fungi can only be gained through a careful study of their teleomorphs.

Gliomastix Guéguen is a genus of *Acremonium*-like Hyphomycetes having dark phialides and conidia. At least one species is the anamorph of a species of *Wallrothiella* Saccardo, a genus of black, sphaeriaceous Ascomycetes (Hughes & Dickinson 1968). Gams (1971) included

Gliomastix as a section of *Acremonium*, but this is acceptable only in a morphologically based system. Since the teleomorphs of *Acremonium* and *Gliomastix* belong in different orders, it is unlikely that the anamorphs have any more than a morphological similarity.

III. SYNNEMATAL, SPORODOCHIAL AND PYCNIDIAL ANAMORPHS

The form-genera represented under this heading produce three kinds of conidiomata: sporodochia in *Tubercularia* Tode ex Fries, *Dendrodochium* Bon., *Myrothecium* Tode ex Fries, and *Kutilakesopsis* Agnihothrudu & Barua; synnemata in *Stilbella* Lindau (including *Stilbum* Tode ex Merat) and *Stromatographium* Höhnel; and pycnidia in *Zythiostroma* Höhnel.

Each of these genera corresponds to one of two stromatic types of anamorph found in the nectrioid fungi. The first is the *Tubercularia*-type, the anamorph of *Nectria cinnabarina* (Tode ex Fries) Fries and its relatives. The second is the *Dendrodochium-Myrothecium*-type characteristic of the *Nectria ochroleuca* (Schw.) Berk.- and *N. ralfsii* Berk. & Br.-groups respectively.

Sporodochia of *Tubercularia vulgaris* Tode ex Fries are red-orange, erumpent and pseudoparenchymatous; phialides arise as terminal branches of hyphae at the surface of the conidioma. The hemispherical conidial mass, at first white, later becomes a bright coral colour. Eventually, after the cessation of conidium production, perithecia form over the surface of each sporodochium. Sporodochia do not develop in pure culture. Colonies are coral-coloured and slimy; the phialides are *Acremonium*-like, arising as scattered, lateral branches of hyphae.

The *Tubercularia*-type sporodochial conidioma has developed in two ways. *T. vulgaris*, the anamorph of *N. cinnabarina*, sometimes produces short synnematal conidiomata (Wollenweber 1926) through elongation of the basal stroma. These cannot be distinguished from the *Stilbella* anamorphs of species such as *Thyronectria pseudotrichia* (Schw. ex Berk. & Curt.) Seeler, which also have coral-coloured conidial masses.

In the second line of development, the convex hymenium of *T. vulgaris* has become concave, expanded and involuted, giving rise to the characteristic red pycnidial conidioma of *Zythiostroma* Höhnel. The hymenium of *Zythiostroma* is involuted and the conidial mass is coral-coloured. These pycnidial conidiomata are produced by species of the *Nectria aquifolii* (Fr.) Berk.-group (Booth 1959).

The *Nectria cinnabarina*- and *N. aquifolii*-groups can be merged, since all the species represent an homogeneous series around *N. cinnabarina*. They have the same perithecium morphology, colour and habitat and, as we have shown, their anamorphs are easily derived from *Tubercularia vulgaris*, the anamorph of *N. cinnabarina*. The resultant group has a wide variety of ascospore forms, but ascospores of most of the species, including *N. cinnabarina* (Brefeld & Tavel 1891) share the tendency to bud either while in the asci or just prior to germination. Ascospores may be didymosporous and budding or non-budding, phragmosporous and budding, scolecosporous and budding, or dictyosporous and budding or non-budding. The included species have been placed in one or more of the following genera: *Creonectria* Seaver (stromatic species with didymosporous ascospores), *Aponectria* (Sacc.) Sacc. (didymosporous ascospores budding), *Chilonectria* Sacc. (didymosporous ascospores budding), *Ophionectria* Sacc. (scolecosporous ascospores), *Scoleconectria* Seaver (stromatic species with

scolecosporous ascospores), *Thyronectria* Sacc. (dictyosporous ascospores, perithecia immersed in a stroma), *Pleonectria* Sacc. (dictyosporous ascospores, perithecia seated on a stroma), *Megalonectria* Speg. (dictyosporous ascospores, anamorph synnematous), as well as others. Apart from the fact that these generic concepts are not mutually exclusive, they separate, into distinct genera, species that are closely related to each other. *Nectria cinnabarina* is the type species of *Nectria*, and if this group is ever accepted as a 'good' genus, it will have to be regarded as *Nectria s. str.* The group, except for the tropical *T. pseudotrichia*, is temperate, occurring on woody plants as weak parasites or early secondary invaders.

The stroma of the *Dendrodochium-Myrothecium*-type anamorph is often not as well developed as that of the *Tubercularia*-type. Conidiophores are loosely united, and phialides arise at the apex of each conidiophore in the form of a penicillus or in whorls. The stroma is usually white and the conidial mass white to pale pink in *Dendrodochium*, and dark green in *Myrothecium*. Cultures usually have abundant, white mycelium in which are found poorly- to well-developed sporodochial conidiomata. Conidiophores in cultures of the *Dendrodochium*-type, whether they are produced singly or united into sporodochial conidiomata, resemble those of *Gliocladium roseum* Bain. which is the anamorph of *Nectria ochroleuca* (Schw.) Berk. *Gliocladium roseum* rarely forms sporodochial conidiomata in nature.

The *Nectria ochroleuca*-group (Samuels 1976a) is one of the largest and most easily recognized groups, but its members are among the most difficult to identify. Perithecia are yellow to orange; perithecial ornamentation differs only in the degree of wall roughness from species to species, and ascospore and conidium measurements for the species overlap in a continuous series ranging from 10-25 µm. The group is almost exclusively tropical in distribution, and most species are found on woody plants, although some occur on herbaceous plants as well. *Gliocladium roseum* is a cosmopolitan anamorph which is a common soil inhabitant and mycoparasite.

Perithecia of *N. ralfsii* and its relatives are similar in structure to those of *N. ochroleuca*. They are yellow to orange, smooth to scaly, and are seated on a previously conidiogenous stroma. The perithecium wall is rather wide and is comprised of *textura angularis* whose cell walls are somewhat thicker than those in the *N. ochroleuca*-group. All species have *Myrothecium* anamorphs. Three species are known to belong to the group, but there are undoubtedly many more members yet to be discovered in the tropics. A recent Venezuelan collection of an unnamed *Nectria* belonging to this group has produced, in cultures derived from single ascospores, more or less free conidiophores with green conidia suggestive of the *Gliocladium catenulatum* Gilman & Abbott-Series as defined by Raper & Thom (1949). It is possible, then, that the basic unit of organization of the *Myrothecium* sporodochial conidioma is *Gliocladium catenulatum*-like, just as the basic unit of the *Dendrodochium* sporodochial conidioma is *Gliocladium roseum*-like. These differ fundamentally from the *Tubercularia* series, which is based on *Acremonium*.

Tulloch (1972) excluded the anamorphs of *N. ralfsii* and *N. pityrodes* from *Myrothecium* because sporodochial conidiomata of these species lack marginal hairs. This exclusion is unwarranted. The only known teleomorphs of *Myrothecium*-like fungi are species of *Nectria*, including *N. bactrioides*, the anamorph of which she included in *Myrothecium*. Because

Myrothecium is an artificial form-genus, and in the absence of other known teleomorphs for the genus, we do not think that the *Myrothecium*-like anamorphs of *Nectria* can be segregated in a separate genus from *Myrothecium* species whose teleomorph is unknown.

Gliocladium roseum and *G. catenulatum* are not like *G. penicillioides* Corda, type species of *Gliocladium* Corda and anamorph of *Hypomyces aureo-nitens* L.-R. Tul. & C. Tul., or *G. deliquescens* Sopp, the anamorph of *Hypocrea* spp. The conidiophore of *G. penicillioides* and *G. deliquescens* is long and graceful, and bears a single, terminal penicillus of phialides from which conidia are produced. The conidia, borne in a terminal mucilaginous droplet, are hyaline in *G. penicillioides* and green in *G. deliquescens*. Conidiophores are never aggregated in sporodochial conidiomata. Conidiophores of *G. roseum* and *G. catenulatum* are short and branched, tending to be aggregated in sporodochioid conidiomata, and produce wet chains of conidia. *Gliocladium roseum* can be referred to *Clonostachys* Corda; the position of *G. catenulatum* is uncertain.

The synnematal conidioma occurs in several unrelated groups of fungi, and synnematous anamorphs are found throughout the nectrioid fungi. The type species of *Stilbella*, *S. cinnabarina* (Mont.) Wollenw., is a derivative of *Tuberculariа vulgaris*. Synnematal conidiomata seemingly identical to those of *S. cinnabarina* are formed by *Nectria aurantiaca* and *Sphaerostilbe repens* Berk & Br. However, on the basis of perithecium wall structure and ascus and ascospore morphology, these species belong in a group with *N. flammea* (Tul.) Dingley, which includes insecticolous species having synnematous *Fusarium* anamorphs (= *Atractium* Link ex Chev., *Microcera* Desm., etc.). The *N. flammea*-group is close to the *N. cinnabarina*-group, and the production of *Stilbella cinnabarina*-like synnematal conidiomata by *N. aurantiaca* and *Sphaerostilbe repens* confirms the close relationship between these two groups.

Anamorphs of *N. flavo-lanata* Berk. & Br. and its relatives are also either sporodochial (*Kutilakesopsis*) or synnematous (*Stromatographium*; see Ciferri 1954). Clavate, golden, granular hairs arise from the perithecium wall, and the ascospores are fusiform and prominently striate. Perithecia arise from the conidiomata. The anamorphs appear to be derivatives of the *Tuberculariа*-type. The sporodochial and synnematal conidiomata are white and have a yellow conidial mass; they produce golden hairs identical to those found on the perithecia, and the conidia are didymosporous.

IV. FUSARIUM ANAMORPHS

Although the genus has been intensively studied, much remains to be done in the taxonomy of *Fusarium* Link ex Fr., the most economically important genus of hypocrealean anamorphs. The most recent and rational treatment of the genus is that of Booth (1971). Our comments on the genus and its relationship are drawn from Dr. Booth's treatise, to which we refer the reader for a complete discussion.

The only known fungi to have *Fusarium* anamorphs fall into the genera *Gibberella* Sacc. and *Nectria*, with far fewer in *Calonectria* de Not. and *Micronectriella* Höhn. Wollenweber (1931), followed by Booth (1971), divided *Fusarium* into several sections, most of which have as their teleomorphs distinctive groups of nectrioid species.

The anamorphs of *Micronectriella* species are in *Fusarium* sect. *Arachnites* Wollenw., whose

macroconidia are small, curved and apedicellate; unlike most fusaria, their conidia do not form on sporodochial conidiomata. The dark, fleshy perithecia of *Micronectriella* are immersed in leaf tissue. Even though ascospores have one or two to three transverse septa, the species are treated in one genus, and not two as would be the case in a classical system, because of their overall similarity in structure and life-cycles (Booth 1964, 1971). Müller (1977) treated *Micronectriella* as a synonym of *Monographella* Petrak, a genus of the Hyponectriaceae, because of its amyloid ascus apex. The systematic position of the Hyponectriaceae is unclear.

Species of *Fusarium* sect. *Episphaeria* Booth are the anamorphs of the *Nectria episphaeria* (Tode ex Fr.) Fr.-group (Booth 1959, 1971), which includes at least one species now placed in *Calonectria*. These fusaria are usually slow growing, salmon-coloured and slimy, lacking aerial hyphae in cultures. Most of the species grow on other pyrenomycetes or loculoascomycetes. The group corresponds, in part, to *Dialonectria* (Sacc.) Cooke, which includes species of *Nectria* having smooth-walled red perithecia seated directly on the substrate. The ascospores of the *N. episphaeria*-group are usually tinted brown and are spinulose or warted. Although *Fusarium* is the predominant anamorph, not all species have *Fusarium* states. *Nectria vegeliniana* (Rehm) Höhn., as it is found in New Zealand, produces a slimy, salmon-coloured *Acremonium*-like anamorph in pure culture. Because *N. episphaeria* and *N. vegeliniana* are closely related in features of perithecia, ascospores and habitat, and because cultures of the two are macroscopically similar, it is possible that the anamorph of *N. vegeliniana* is a *Fusarium* that forms only microconidia. *Nectria vilior* and *N. cosmariospora*, discussed earlier, produce green anamorphs that are intermediate between *Acremonium* and *Verticillium*. *Nectria consors* (Ell. & Ev.) Seaver has a *Volutella* Tode ex Fr. anamorph (Samuels 1977), but its perithecia are distinct from those of *Pseudonectria rousseliana* (Mont.) Seaver (Bezerra 1963) and *P. pachysandricola* Dodge (Dodge 1944), both of which also have *Volutella* anamorphs.

Synnematous fusaria, included at various times in *Atractium*, *Microcera*, *Pseudomicrocera* Petch, *Stilbella* and *Fusarium*, are formed by the *Nectria flammea*-group (Booth 1959, 1971). The conidiomata are very distinctive both in morphology and in habitat. Before maturity the apex of the sporodochium or synnema is enclosed by hyphae, but when the *Fusarium* macroconidia are mature the apex becomes discoidal, exposing a bright orange hymenium. Perithecia form at various levels toward the base of the stalk. Most species in the group are parasites of scale insects, but *Nectria jatrophae* (Möller) Wollenweber, *N. aurantiaca*, and *Sphaerostilbe repens* are found on wood. The anamorphs of *N. aurantiaca* and *S. repens* are typical members of the form-genus *Stilbella*, similar to the *Stilbella* state of *Thyronectria pseudotrichia*. However, perithecium morphology places them in this group of insect parasites that have *Fusarium* anamorphs. All the species in the *N. flammea*-group have previously been placed in *Sphaerostilbe* Tulasne or *Corallomyces* Berk. & Curt., genera described for species of *Nectria* having synnematous anamorphs. The type species of both *Sphaerostilbe* (*N. flammea*) and *Corallomyces* (*C. elegans* Berk. & Curt. = *Sphaerostilbe repens*) are included here. Species of nectrioid fungi having synnematous anamorphs are not necessarily related, and the generic names *Sphaerostilbe* and *Corallomyces* are no longer used. However, the group of species having synnematous, fusarial anamorphs circumscribed here is homogeneous. If this group were

to be recognized at generic rank, *Corallomyces*, the older but lesser known name, would have to be applied.

The genus *Gibberella* accounts for nearly half the fungi having *Fusarium* anamorphs. Although similar to *Nectria*, especially *N. haematococca*, *Gibberella* is a uniform and distinctive genus having dark blue to purple, fleshy perithecia and phragmosporous ascospores. Approximately half of the sections of *Fusarium* recognized by Wollenweber (1931) and Booth (1971) contain anamorphs of *Gibberella*, and Wollenweber considered those sections to occupy a central position within *Fusarium*. Most of the *Gibberella* anamorphs are easily recognized sections of *Fusarium* based on cultural characters (sects. *Lateritium* Wollenw., *Discolor* Wollenw.), distinctive conidium morphology (sect. *Gibbosum* Wollenw.) or the ability to produce microconidia from polyphialides (sects. *Arthrosporiella* Wollenw. & Reink., *Liseola* Wollenw.). These sections do not bear any obvious relationship to each other, except that they are unquestionably species of *Fusarium* and that they are anamorphs of *Gibberella*. Wollenweber (1931:321) said that, even though there are major differences in the conidium morphology of these groups, they are closely related in having the same teleomorph.

Two additional nectrioid fungi having *Fusarium* states deserve comment. *Calonectria rigidiuscula* (Berk. & Br.) Sacc. is a common tropical species and is found both as a saprophyte and as a parasite on a wide variety of substrates. This species, with its pallid, strongly warted perithecia, shows similarities to both *Gibberella* and *Nectria haematococca* Berk. & Br., but does not seem to have any close relatives for which anamorphs are known. Its anamorph, *Fusarium decemcellulare* Brick, was maintained in the isolated section *Spicarioides* Wollenw. et al. by Booth and Wollenweber. *Calonectria rigidiuscula* is a tropical species, and future collecting in the tropics may disclose the affinities of the species.

Among the best known of the fusaria is *F. solani* (Mart.) Sacc., the anamorph of *Nectria haematococca*. The only known species closely related to *N. haematococca* are *N. illudens* Berk. and *Ophionectria trichospora* (Berk. & Br.) Sacc. (Rossman 1975, 1977). The anamorphs of *N. haematococca* and *N. illudens* are found in *Fusarium* sect. *Martiella*. Booth (1971) included two other fusaria in this section, one of which is the anamorph of *Nectria ventricosa* Booth. However, the *Fusarium* state of *N. ventricosa* does not belong in this section, and the teleomorph does not appear to be related to either *N. haematococca* or *N. illudens*. Wollenweber (1926) included *N. haematococca* in *Hypomyces* because it produces chlamydospores, as do the *Sepedonium* anamorphs of many species of *Hypomyces*. Wollenweber seems to have overlooked every other feature in the life cycles of *Nectria* and *Hypomyces* in placing *N. haematococca* in the latter genus.

Rossman (1975) has recently shown that *N. haematococca* and the scolecosporous species *Ophionectria trichospora*, the type species of *Ophionectria*, are closely related to each other and could probably be treated in the same genus. The anamorph of *O. trichospora* is *Antipodium spectabile* Pirozynski (Pirozynski 1974). *Antipodium* is an interesting, monotypic genus of the Hyphomycetes that has phialoconidia which are *Fusarium*-like, except that the "foot cell" is at the conidium apex. Pirozynski suggests that *A. spectabile* might be related to *Fusarium* to *Eriomycopsis* Speg. The latter is the anamorph of some brightly coloured, bitunicate Ascomycetes, and bears its conidia on denticles. Since *O. trichospora* is closely

related to *N. haematococca*, and since the phialoconidia of the two fungi have the same basic morphology, we believe that *Antipodium* and *Fusarium* are indeed related.

V. CYLINDROCARPON ANAMORPHS

Cylindrocarpon Wollenw. differs from *Fusarium* in having macroconidia that lack a foot cell. As with *Fusarium*, the only teleomorphs known for *Cylindrocarpon* are nectrioid.

There is no complete monograph of *Cylindrocarpon*. The most recent, and most usable, partial monograph is that of Booth (1966). He divided the genus into groups based on the presence or absence of macroconidia, microconidia and chlamydospores. It is unclear whether those groups reflect natural relationships.

Ascomycetes having *Cylindrocarpon* anamorphs belong to one of four main groups, the *Nectria coccinea* (Pers. ex Fr.) Fr.-group (Booth 1959), the *N. mammoidea* Phillips & Plowr.-group (Booth 1959), the *N. radicicola* Gerlach & Nilsson-group, and the *N. arenula* (Berk. & Br.) Berk.-group (Booth 1959, Samuels 1978). The first three of these groups are probably closely related to each other, and the *N. mammoidea*- and *N. coccinea*-groups intergrade. Booth (1966) treated *N. radicicola* in the *N. coccinea*-group, but *N. radicicola*, *N. coprosmae* Dingley and *N. tawa* Dingley represent a closely knit group of species that can easily be identified apart from *N. coccinea*. The anamorphs of these fungi are characteristic of *Cylindrocarpon* in that they form macroconidia, microconidia and chlamydospores, and in that the macroconidia usually arise from pionnotes.

The *N. coccinea*- and *N. mammoidea*-groups are well known in temperate regions, but many additional species, especially of the *N. coccinea*-group, will be found at tropical latitudes. In the neotropics we have collected several unidentified *Nectria coccinea*-type specimens which have phragmosporous ascospores and are constantly associated with *Cylindrocarpon* anamorphs on the host.

The fourth group of *Cylindrocarpon*-producing fungi, the *N. arenula*-group, is not allied to the previous three either in perithecium or conidium morphology. The perithecia are orange, and their wall structure is unlike that found in the *N. coccinea*-, *N. mammoidea*- and *N. radicicola*-groups. Most of the species currently included in this group have phragmosporous ascospores, although the ascospores of *N. arenula* itself are didymosporous. The *Cylindrocarpon* anamorphs lack microconidia and chlamydospores, and the usually unbranched conidiophores are not aggregated, arising freely in the aerial mycelium or directly from the substrate in nature, thus having an *Acremonium*-like aspect. At least one species of the group, *N. arenuloides* Samuels, actually has an *Acremonium* anamorph.

VI. CYLINDROCLADIUM ANAMORPHS

The conidiophores of *Cylindrocladium* Morgan are penicillately branched at the apex, and a long, sterile prolongation with a characteristic tip arises from each penicillus. Conidia of *Cylindrocladium* are straight, narrowly cylindrical, and didymosporous or phragmosporous. Although conidiogenesis is usually regarded as phialidic, many illustrations [Alfieri et al. 1970, fig.2, Sobers 1968, fig. 1, Sobers & Seymour 1967, fig. 3, Matsushima 1971, figs. 144-148, and Booth 1966, fig. 24 of *Cylindrocarpon retaudii* (Bugn.) Booth which is probably a

species of *Cylindrocladium*], suggest a holoblastic type of conidiogenesis for some species. Only within the past fifteen years has the pathogenic potential of *Cylindrocladium* been widely recognized. One result of this recognition has been a proliferation of names for both teleomorphs and anamorphs. The only treatments of the group are by Boedijn & Reitsma (1950) and Peerally (1974), and many species were beautifully re-described and illustrated by Matsushima (1971, 1975). Some of the newly proposed names for the teleomorphs apply to older species, such as *Nectria gigantospora* Zimmerman, which were described as tropical saprophytes.

The *Cylindrocladium*-producing Ascomycetes form a well defined group in teleomorph and anamorph morphology and habitat. Perithecium wall structure is similar to that of *N. radicicola*. The ascospores may be didymosporous or phragmosporous, and fusiform to inequilaterally fusiform. The species have been placed in *Nectria*, *Calonectria* and *Neonectria* Wollenweber, a genus proposed to accommodate those Nectriaceae having didymosporous or phragmosporous ascospores. Today they are regarded as species of *Calonectria*. The group is in need of taxonomic revision, with close attention being paid to the older literature.

CONCLUSIONS

Pyrenomycetes are divided into genera largely on the basis of single characters. The resultant system is both artificial and impractical. It is artificial in that species which share several characters are separated by the excessive emphasis given to individual features such as ascospore septation. It is impractical because taxa based on single characters are rarely mutually exclusive.

The nectrioid fungi are now among the best known of the Pyrenomycetes. These fungi demonstrate a wide diversity both in teleomorphs and anamorphs. The patterns of development found in these fungi suggest that several natural groups exist. Representatives of these groups share the greatest number of characters possible, and definitions of the groups cross classical generic lines. Some of the groups are now recognized as distinct genera, for example *Gibberella* and *Micronectriella*. Other groups could be given generic status because of their distinctiveness, such as the *Nectria peziza*-group, or those species having *Cylindrocladium* anamorphs. We regard *Nectria* as a very large genus with several more or less well-defined groups of species, which could possibly be recognized as subgenera. Species of *Thyronectria*, *Calonectria*, *Sphaerostilbe* and other segregate genera can be transferred to *Nectria* and placed alongside corresponding species within that genus.

Taxonomy of Fungi Imperfecti is based on convenience. We now recognize several distinct types of conidium development, and can divide the Fungi Imperfecti into large groups of ontogenetically similar species. Within these large groups, however, it is difficult to recognize relationships; for example, nobody would ever suggest that all fungi having a phialidic ontogeny are closely related. Knowledge of ascomycetous life-cycles can lead to the recognition of natural groups of Fungi Imperfecti. Ascomycetes having similar perithecium morphology also tend to have morphologically similar anamorphs. Thus, one can speculate with some chance of being correct both about the type of anamorph belonging to an Ascomycete, and also about the relationship of a conidial fungus to a teleomorph and to other anamorphs whose

teleomorphs are known.

DIALOGUE FOLLOWING DRS. SAMUELS AND ROSSMAN'S PAPER

SUBRAMANIAN: What are the relationships of *Acremonium*, *Monocillium* and *Torulomyces*?

VON ARX: According to Gams, *Torulomyces* is a simplified *Penicillium*-like anamorph with dry conidia. The other two genera have slimy conidia. Gams considers *Monocillium* to be *Acremonium*-like but with a thick-walled stalk. He saw about 10 species of *Monocillium* and noted *Niesslia* teleomorphs for about half of them. He found *Gliomastix*-like fungi that were absolutely colourless, and *Acremonium*-like fungi with dark pigment in the conidia, but not in the hyphae. It seems that here you cannot rely on presence or absence of pigment to separate genera, and I do not use pigment alone as a justification for a genus.

KENDRICK: Samuels & Rossman show the evolution of their anamorphs as progressing through time from the simple to the complex. I would merely like to inject a note of caution: we cannot be sure that evolution has not, as Dr. Malloch so cogently suggested, moved in the opposite direction. We must perhaps ignore the direction of the arrows. Nevertheless I have no doubt that these anamorphs are in fact related, and I compliment the authors on the clear, rational and well-illustrated way in which they have presented their data. It is an excellent contribution to the expressed aims of this conference.

SAMUELS: The more I think about it, the more I think that the arrows should be pointing in the other direction anyway, toward *Acremonium* and *Gliocladium*. I don't know enough yet to say that any group of *Nectria* species is more or less highly evolved than any other group within the genus. It is interesting, however, that within the conidiomata there are at least two possible branching patterns. The *Tubercularia* types have a pattern of more or less randomly spaced phialides along a central axis. In culture, those that do not produce complex conidiomata, produce *Acremonium*-like conidiophores. The *Dendrodochium* types have a penicillate branching pattern within their sporodochia, and in culture they produce free, *Gliocladium*-like conidiophores.

SUBRAMANIAN: It is convenient to maintain the three hyaline, phragmoconidial genera, *Fusarium*, *Cylindrocarpon* and *Cylindrocladium*, but I have noticed that after you keep them in culture for a long time, they tend to produce only microconidia, which gives them a very *Acremonium*-like aspect. Sometimes, as in the anamorph of *Neocosmospora vasinfecta*, the form may be intermediate between *Acremonium* and *Fusarium*.

VON ARX: We reserve the name *Acremonium* for forms with narrow hyphae and narrow phialides. Things like anamorphic *Neocosmospora* we simply call microconidial states of *Fusarium*. Booth introduced the genus *Micronectriella*, but Müller and I have studied the type, and found it to be bitunicate, and a synonym of *Sphaerulina* (Mycosphaerellaceae). Another '*Micronectriella*' is actually the type species of the genus *Plectosphaerella* Klebahn, a good genus exactly intermediate between Hypocreaceae and Sphaeriaceae because it is *Nectria*-like, but has dark perithecia. Another '*Micronectriella*' studied by Müller is

Nectria-like, but has amyloid asci and represents the genus *Monographella* of Petrak. So *Micronectriella* sensu Booth is heterogeneous.

SAMUELS: *Micronectriella* demonstrates very well the difficulty in using single characters to classify fungi. *Micronectriella* was classified with *Nectria* because of its *Fusarium* anamorph. This classification went unchallenged for many years. It was only through the very careful, species by species studies made by Müller & Arx that the true nature -- or natures -- of *Micronectriella* came to light. It seems to me that the only way we will ever develop a rational system of fungal taxonomy is to take nothing for granted, but to make detailed studies of as many aspects of individual species as is possible.

PIROZYNSKI: The genus *Tuberculispora* may disturb the system a little. It has sympodially proliferating conidiogenous cells, and it has been found three times closely associated with hyperparasitic species of *Nectria*. The evidence here is still only circumstantial. Samuels has, perhaps legitimately, left it out, but I would appreciate his comments on this.

SAMUELS: I have found *Tuberculispora jamaicensis* in association with *Nectria leucorrhodina* more than once. I have tried to culture the *Nectria* but have not been successful. It is not uncommon to find more than one hyperparasite in the same spot; perhaps the *Tuberculispora* is a hyperparasite of the *Nectria*. I would be surprised to find such a holoblastic conidiogenesis in *Nectria*.

WEBSTER: Other omissions are the *Flagellospora* and *Heliscus* anamorphs of *Nectria* species -- though these, it must be noted, are phialidic.

SAMUELS: I do not know either *Nectria penicillioides* Ranzoni (teleomorph of *Flagellospora*) or *N. lugdunensis* Webster (teleomorph of *Heliscus*). From their descriptions (which are really good!), both species appear to be related to the *Nectria episphaeria* group. Many species of this group have *Fusarium* states, and my guess is that *Flagellospora* and *Heliscus* are derivatives of *Fusarium*. There are still many nectrias yet to be found and it is certain that many of them will have anamorphs that cannot be easily fitted into the scheme that we've presented here. That's one of the things that makes this work so much fun. The *Nectria episphaeria* group is probably heterogeneous; all those little red nectrias that don't have *Cylindrocarpon* states seem to get dumped here! We need to know a lot more life histories before we can make real progress in the taxonomy of this group.

SUBRAMANIAN: Didn't Tubaki connect a *Trichothecium* to a *Nectria*?

SAMUELS: Tubaki described *Hypomyces trichothecoides* and its *Trichothecium* anamorph. I do not know of any connection between *Nectria* and *Trichothecium*. There is no doubt that *H. trichothecoides* is a species of *Hypomyces*. It is very difficult to distinguish between *H. trichothecoides* and *H. aurantius* on the basis of perithecial morphology alone, but *H. aurantius* has a *Cladobotryum* anamorph.

WATLING: *Fusarium nivale* causes considerable damage to cereals including barley in Scotland, and therefore to the whisky industry. The teleomorph has undergone several name changes. Could someone give me an up-to-date report on this situation?

MÜLLER: The teleomorph was originally thought to be a *Calonectria*. But we saw that the perithecia develop immersed in the host, the wall is pigmented, and the ascus apex is

amyloid. So it could not be a *Calonectria*. We thought it could be a *Griphosphaeria*, but this was then reduced to synonymy with *Discostroma*. We now know that the connection with *Discostroma* was not correct. Then Booth thought it was a *Micronectriella*; von Arx has already told you why that is wrong. I checked two Petrak genera occurring on grasses, *Monographella* and *Griphosphaerella*. It turned out that these were both identical with the teleomorph of *Fusarium nivale*, so the older name, *Monographella*, is the correct one.

WATLING: So this would be put in the family Amphisphaeriaceae?

VON ARX: Yes, this is one of those awful intermediates. The family is not very natural, as yet.

WATLING: I ask these questions because I think *Fusarium nivale* is so different from the other Fusaria I see.

MÜLLER: Someone should look at *F. nivale* very carefully, because it seems to me that it may not be phialidic, but annellidic. If that were so, it would fit in with *Seimatosporium* and other anamorphs of *Discostroma*, etc., and fit better in the Amphisphaeriaceae.

VON ARX: In my opinion, *Discostroma* and *Monographella* are morphologically extremely similar -- they just have different anamorphs.

WATLING: I'm concerned that we should put the right name on this teleomorph because the plant pathologists get very fed up with the name changes.

VON ARX: Use only the name *Fusarium*!

KENDRICK: But it may not be a true *Fusarium*. Neither the anamorph nor the teleomorph is immune to name changes. You can't protect yourself by simply using the name of the anamorph.

WEBSTER: Does anyone know what happened to *Nectria inventa* Pethybridge and its verticillate anamorph?

VON ARX: No one has seen it since it was originally described. It needs to be repeated.

It is not surprising that we know so much, relatively speaking, about the groups discussed in the last three chapters, because they have been the subjects of repeated taxonomic scrutiny during this century. But it is refreshing and encouraging to learn in the next chapter that even in a long-neglected group such as the Coelomycetes, anamorph-teleomorph connections are now being given the attention they deserve.....

12
Some Coelomycetous Anamorphs and Their Teleomorphs

T.R. Nag Raj

ABSTRACT

New reports of affinities between some Coelomycetes and Ascomycetes include: *Harknessia* sp. (originally described as *Mastigonetron fuscum*), *H. thujina* and *Mastigosporella hyalina* with *Physalospora** spp. (Diaporthaceae); *Pestalotiopsis* sp. with *Pestalosphaeria* sp. (Amphisphaeriacae); *Seimatosporium dilophosporum* with an undescribed genus close to *Broomella* (Amphisphaeriaceae); *Ciliochora longiseta* with *Phyllachora* sp. (Polystigmataceae); *Cryptosporiopsis* sp. with *Melchioria** sp. (Sphaeriaceae); *Coma circularis* with *Rhopographus** sp. (Stigmateaceae); and a few members of an undescribed form-genus with *Phacidium* spp. (Phacidiaceae). A brief account of a Coelomycete bearing clamp connections is included.

INTRODUCTION

About 1350 form-generic names have been proposed for Coelomycetes. Some of these are large, with several hundred species (e.g., *Phoma, Septoria,* etc.); some others are heterogeneous mixtures of many species exhibiting different modes of conidium ontogeny (e.g., *Septogloeum, Septoria,* etc.); in many, details of conidium ontogeny are still unknown in the type species. In effect, we have a very obscure picture of Coelomycete taxonomy in terms of modern criteria of conidium ontogeny correlated with morphology: some of the form-genera are well delineated, while the relationships of a good number of others are relatively unknown. It is thus inevitable that the teleomorph-anamorph connections reported in early mycological literature should include some anomalies. Dealing with the nomenclatural status of 1485 generic names of coelomycetous and pycnothyriaceous fungi, Sutton (1977) rejected 720 and accepted 393. This left 372 generic names still to be re-evaluated. Since Sutton's re-assessment of these genera is limited to the type species, a meaningful analysis of the existing data concerning teleomorph-anamorph connections will be possible *only after* the vast number of old Coelomycete taxa have been reassessed.

If one studies collections of Ascomycetes or Basidiomycetes, one will frequently observe anamorphs. If the collections are fresh, then there is an opportunity to establish the gen-

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* Provisional identifications only. Detailed taxonomic and nomenclatural accounts of these taxa will be published elsewhere.

etic connections between the teleomorphs and the anamorphs by cultural studies. On the other hand, where very old and, therefore, dead collections are involved, presumptive relationships may still be postulated from several other kinds of evidence:

(1) There may be intimate association of the anamorphs and teleomorphs (though here one must consider the possibility of mycoparasitism);

(2) the probability of true relationship is improved if the consistent association between the states is observed in collections from widely separated geographic locations (e.g., *Ypsilonia-Acanthotheciella* -- see Nag Raj 1977);

(3) Sporulating structures of both states may arise from the same mycelium;

(4) Architectural or developmental similarities between the two states may indicate affinity, particularly if the two are closely associated in nature.

Most of the connections reported here are postulated mainly on the basis of these four kinds of evidence.

HARKNESSIA, MASTIGOSPORELLA (COELOMYCETES) AND *PHYSALOSPORA* (DIAPORTHACEAE). In a monographic account of *Harknessia*, Sutton (1971) characterized the members of the form-genus as possessing simple, unilocular, separate or aggregated, immersed or semi-immersed, stromatic pycnidial conidiomata with furfuraceous ostioles; simple, long, lageniform, hyaline, non-proliferating, holoblastic conidiogenous cells; variously shaped, brown, occasionally longitudinally striate, guttulate conidia with part of the conidiogenous cell persisting as a basal appendage, and, in some species, a short, filiform, cellular, apical appendage. Species of *Harknessia* described by Ellis & Everhart included *H. hyalina*, which differed from the other species in possessing hyaline conidia bearing long apical appendages. Höhnel (1914) believed these distinctions adequate to separate the taxon from other species of *Harknessia* at generic level and proposed the name *Mastigosporella* for it, an opinion endorsed by Morgan-Jones (1975) and Sutton (1977). Morgan-Jones (1975) suggested that in addition to the possession of hyaline conidia, *Mastigosporella* differed from *Harknessia* in its blastic-phialidic mode of conidiogenesis (but see below).

The form-generic name *Mastigonetron*, type species: *M. fuscum* Kleb., is attributed to Klebahn (1914), who found the fungus in association with *Pestalotia versicolor* Speg. var. *guaranitica* Speg. in the exsiccatum distributed by Rick as 'Fungi Austro-americani #255'. Höhnel (1914) and Petrak (1950) accepted *Mastigonetron* for species with a long, hyaline, apical conidium appendage, considering this a distinct generic character, because species of *Harknessia* lacked such appendages. Sutton (1971) however, considered *Mastigonetron* a synonym of *Harknessia*.

Klebahn (1914) observed and illustrated an Ascomycete, which he thought was probably a species of *Mycosphaerella*, associated with *Mastigonetron fuscum*. Petrak (1950b) believed that the teleomorph of *Harknessia* was recognizable as a *Cryptosporella*, though he used the name *Mastigonetron* for the anamorph; he reported *C. farinosa* (Ell.) Sacc. (≡ *Valsa farinosa* Ell.) and *C. beltsvillensis* Petr. as the teleomorphs, with *Mastigonetron caudatum* (Ell. & Ev.) Höhn. (≡ *Harknessia caudata* Ell. & Ev.) and *M. affine* (Ell. & Ev.) Petr. (≡ *H. affinis* Ell. & Ev.) respectively as the anamorphs, the relationship being inferred from the close association between the two states.

Recent studies (Nag Raj & DiCosmo, unpubl.) have shown an intimate association of teleomorphs referable to *Physalospora* with *Harknessia affinis*, the groups of ascomata often originating immediately below the conidioma (Fig. 12.1A), with *Mastigonetron fuscum* (Fig. 12.1C,D), and with *Harknessia thujina* (Figs. 12.1E, 12.2A). In the specimens of *H. caudata* in NY, only the spermatial state was associated with the anamorph. In addition, the teleomorph associated with *Mastigosporella hyalina* (Figs. 12.2B-D) is identifiable as *Physalospora quercifolia* Ell. & Ev.

Sutton (1971) included *Mastigonetron fuscum* and *H. affinis* in the synonymy of *Harknessia americana*. According to our studies, *H. americana*, *H. affinis* and *M. fuscum* are distinct species of *Harknessia* differing from each other not only in the morphological features of the conidiomata and the conidia, but also in the details of the teleomorphs associated with the last two species. Other notable features of *Harknessia* spp. relate to the conidiogenous cells and the basal appendages. The conidiogenous cells in most species proliferate percurrently, often three to five times. The basal appendage on the conidium arises as an integral part of the young conidium, the main body of the developing conidium becoming swollen, coloured, thick-walled and separated from the basal (and, where present, apical) appendages by septa at maturity. We interpret conidiogenesis in *Harknessia* as blastic-phialidic. At present, our studies of this group of fungi are still not complete, but the occurrence of *Physalospora* teleomorphs in association with *Harknessia* anamorphs, in at least three different taxa, and on collections originating in geographically disparate areas, is a strong indication of the relationship between the two states. Occurrence of a similar teleomorph in the material of *Mastigosporella hyalina* suggests a very close affinity of *Mastigosporella* with *Harknessia*, from which it differs only in the absence of pigmented conidia and basal appendages.

PESTALOTIOPSIS SP. (COELOMYCETES) AND *PESTALOSPHAERIA* (SPHAERIALES).

Barr (1975) established the connection between a member of the Amphisphaeriaceae and *Pestalotiopsis guepini* (Desm.) Stey. var. *macrotricha* (Kleb.) Sutton, and proposed the generic name *Pestalosphaeria*, type species: *P. concentrica* Barr, to accommodate the teleomorph. In culture, single spore isolates from ascospores and conidia yielded the anamorph. *Pestalosphaeria* was characterized as possessing depressed globose, immersed perithecia with a short erumpent apex and a periphysate apical canal, hyphae emanating from the wall forming a slight clypeus around the apex; stipitate, cylindrical, unitunicate asci with amyloid apical annulus and a chytinoid pulvillus, intermixed with paraphyses; ascospores ovoid-elliptic, 2-septate, light dull brown, with the wall ornamented by 5 or 6 irregular longitudinal ridges.

Montagne (1850) described *Pestalotia americana* as having 3-celled, ellipsoid conidia, but illustrated unicellular, ellipsoid, dark, uni-guttulate conidia bearing an attenuated apical appendage and a rather broader basal appendage. The conidia were indicated as originating in pycnidia. Guba (1961) asserted that the fungus was more properly *Mastigonetron fuscum*, a binomial that was reduced to synonymy with *Mastigonetron americanum* by Balfour-Browne (1968). Sutton (1971) did not find the fungus on the type specimen. He accepted the conclusions of Guba and Balfour-Browne, but transferred the epithet to *Harknessia* as *H. americana*.

A study of the type specimen of *P. americana* has revealed the presence of *Harknessia americana* as well as a *Pestalotiopsis*, the latter associated with an Ascomycete congeneric with

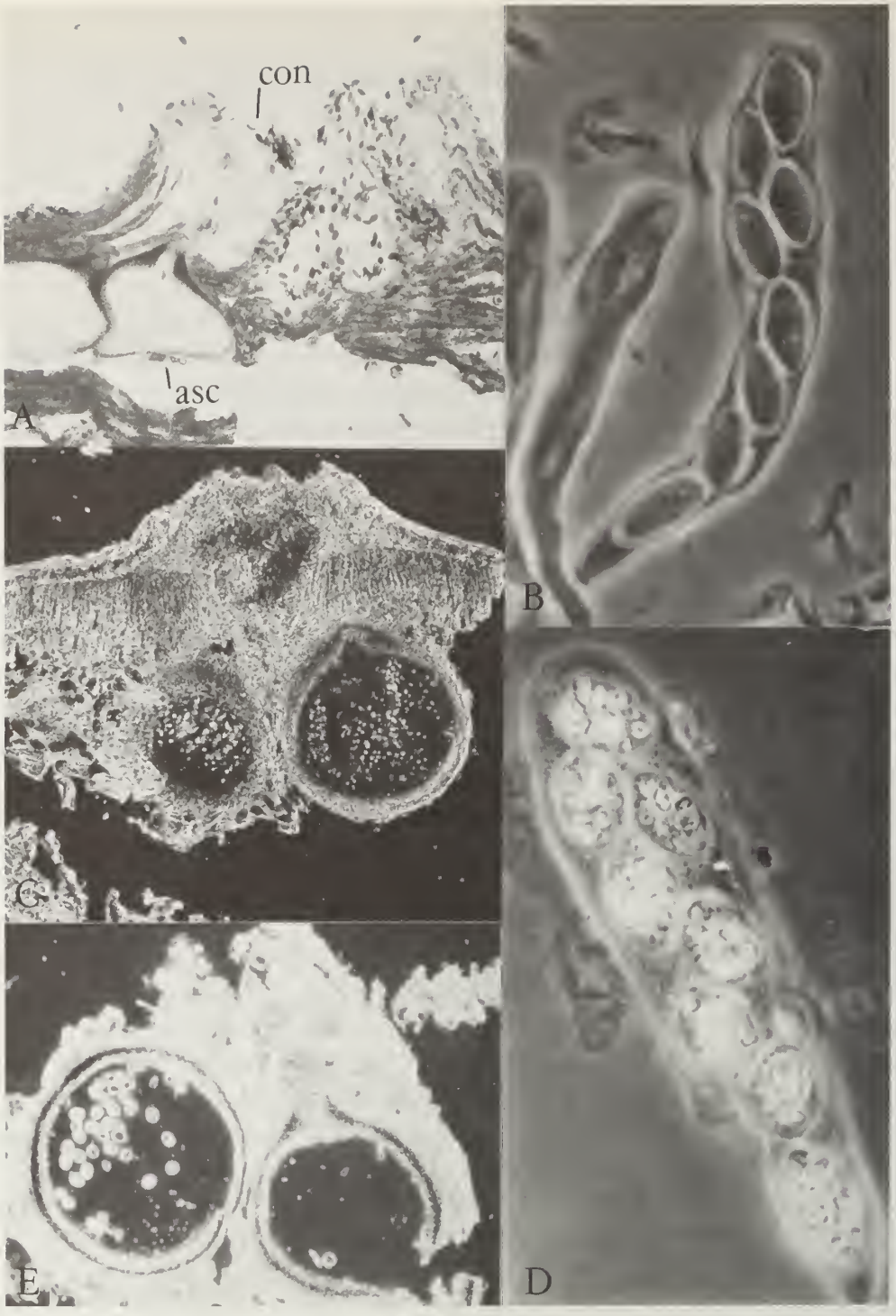

Fig. 12.1 Teleomorphs associated with *Harknessia affinis, Mastigonetron fuscum* and *H. thujina*. A, sectional view of ascoma (asc.) and conidioma (con.) present in material of *H. affinis*. B, mature ascus of the teleomorph in Fig. 1 A. C & D, sectional view of an ascoma, and mature ascus, of teleomorph associated with *Mastigonetron fuscum*. E, sectional view of ascoma of teleomorph associated with *H. thujina*.

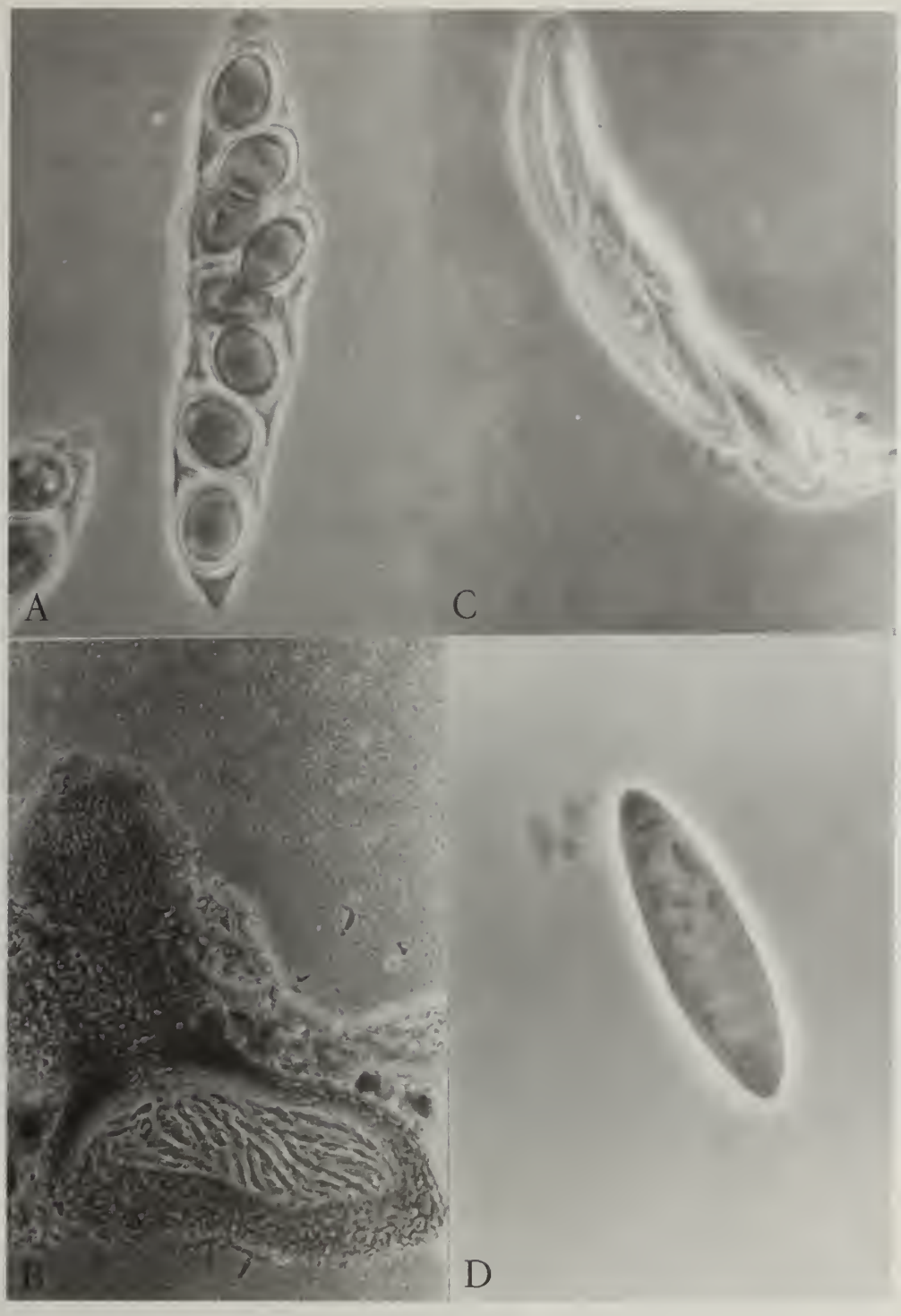

Fig. 12.2 Teleomorphs associated with *Harknessia thujina* and *Mastigosporella hyalina*. A, mature ascus of the teleomorph associated with *H. thujina*. B-D, sectional view of an ascoma, ascus, and an ascospore of the teleomorph associated with *Mastigosporella hyalina*.

Pestalosphaeria concentrica (Amphisphaeriaceae) (Figs. 12.3A-C). It differs from *P. concentrica* in possessing smaller ascomata with narrower walls, longer and wider asci, and slightly larger, verruculose ascospores lacking longitudinal ridges on the walls. The anamorph is an unnamed taxon, but is close to *Pestalotiopsis sydowiana* (West.) Stey., *P. triseta* (M. & Mme. Moreau) Stey., and *P. glandicola* (Cast.) Stey. The relationship between the two states is inferred here from their close association.

SEIMATOSPORIUM DILOPHOSPORUM (COELOMYCETES) AND ITS TELEOMORPH.

The form-genus *Allelochaeta* Petr. and the single species, *A. gaubae* Petr., have been added to the synonymy of *Seimatosporium* and *S. dilophosporum* (Cooke) Sutton, respectively (Nag Raj 1978). The type specimen of *A. gaubae* also bears abundant fructifications of an Ascomycete (Fig. 12.4A-D) very intimately mixed with the anamorph. The perithecia are scattered to densely gregarious, immersed, globose to depressed globose, unilocular, glabrous, ostiolate, with a pseudoparenchymatous wall which is thick, stromatic and seemingly clypeate around the apex. The octosporous asci are cylindric, unitunicate with a non-amyloid apical apparatus, hyaline and intermixed with septate, hyaline paraphyses. The ascospores are uniseriate, elliptic, 2-3-septate, hyaline, without constrictions at the septa or ornamentations on the wall and lack appendages. These features fit in well with the characteristics of the Amphisphaeriaceae sensu stricto. The teleomorph resembles *Broomella* but lacks pigmentation and appendages on the ascospores. Further, the four known species of *Broomella* have anamorphs in *Pestalotiopsis*. Apparently the fungus belongs in a new and as yet undescribed genus. I have learned from Dr. H.J. Swart, Melbourne, Australia, that he has several other taxa that belong in this genus with related anamorphs in *Seimatosporium*, the relationship having been established in pure culture studies.

The generic concept developed for *Seimatosporium* in recent years (Sutton 1964, 1975a,b) is overly broad and appears to include discordant elements. Until recently *Seimatosporium* was considered to contain the anamorphs of *Paradidymella* and *Clathridium* (Barr 1975). Brockmann (1975) segregated the anamorphs of *Discostroma* (= *Clathridium*) into *Seimatosporium* (species with appendaged conidia) and *Sporocadus* (species without conidium appendages). In the taxonomic treatments of *Seimatosporium* the degree of stroma development and the degree of branching of the conidiophores have been ignored. With such information, and additional data on the teleomorphs, it is to be hoped that identification of *Seimatosporium* and related form-genera will become simpler and clearer in the not too distant future.

CILIOCHORA LONGISETA (COELOMYCETES) AND *PHYLLACHORA* (SPHAERIALES)

Höhnel (1919) proposed the form-generic name *Ciliochora* to accommodate a fungus originally described as *Neottiospora longiseta* Racib. Nag Raj & Kendrick (1972) could not find the fungus on the original specimen housed in FH. However, the discovery of another specimen in BPI labelled *Robillarda* sp., and originating from the Philippines, has led to a reappraisal of the form genus. The BPI specimen consists of several leaves bearing numerous scattered, oval to irregular spots with chocolate coloured margins and glistening black central areas. In a sectional view of the infected tissue, the entire thickness of the leaf is seen to be filled with a fungal stroma, with the conidiomata or the ascomata occupying the central part of the

Fig. 12.3 *Pestalosphaeria* sp. and *Pestalotiopsis* sp. present in material of *Harknessia americana*. A-C, sectional view of an ascoma, a mature ascus, and a sectional view of a conidioma.

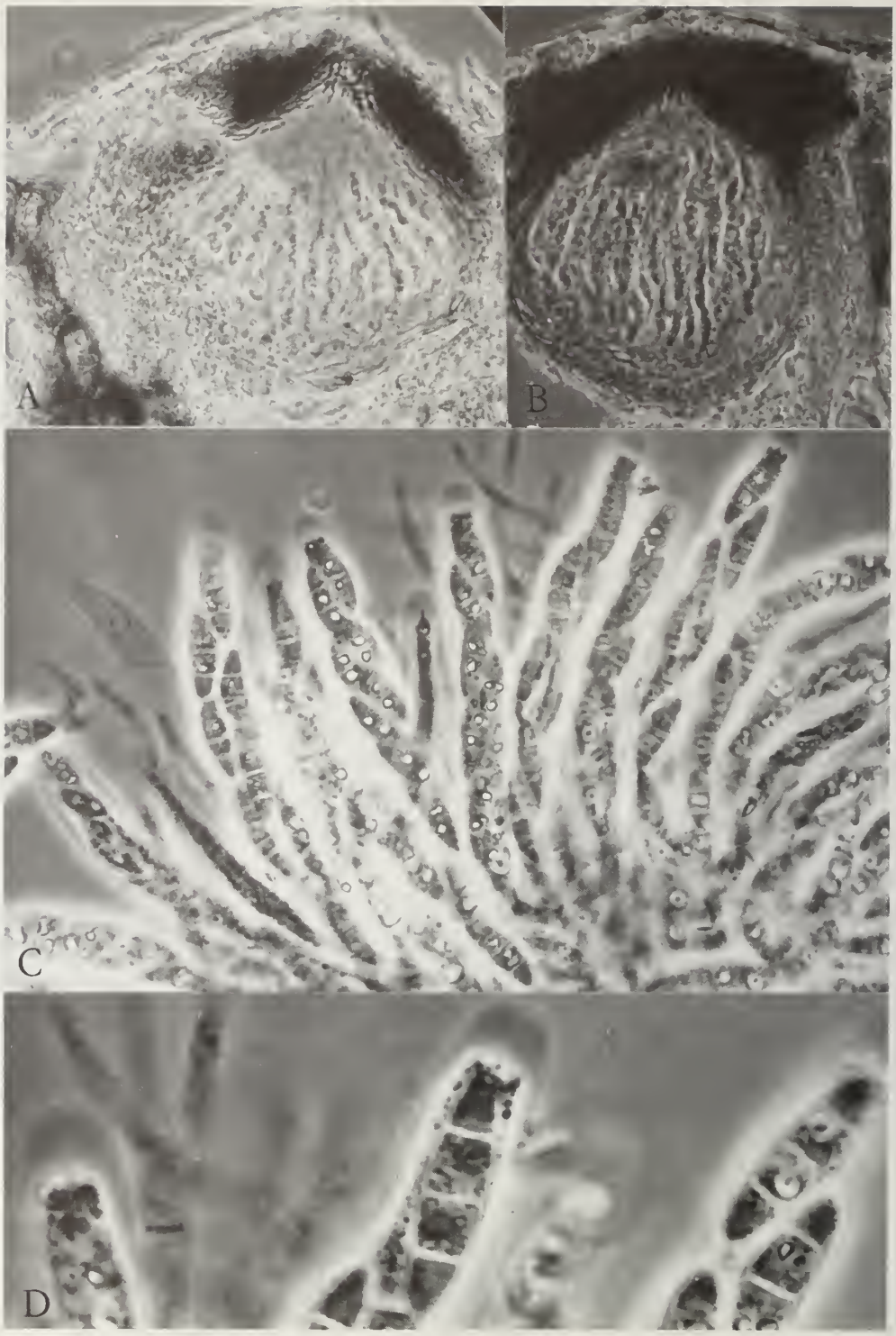

Fig. 12.4 Teleomorph associated with *Seimatosporium dilophosporum (=Allelochaeta gaubae)*. A-D, sectional views of the ascomata, mature asci with paraphyses, and ascospores.

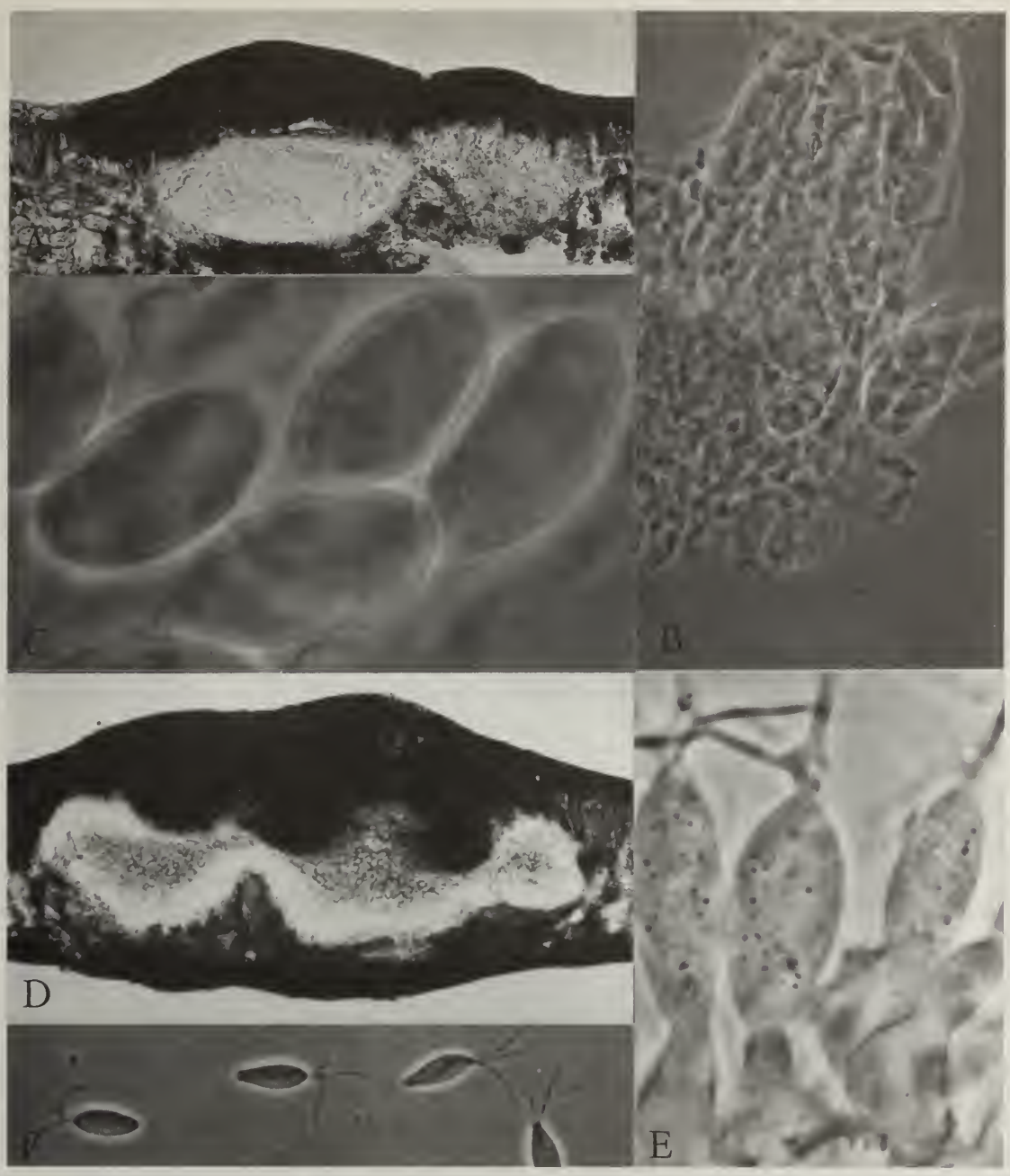

Fig. 12.5 *Phyllachora* sp. and *Ciliochora longiseta*. A-C, sectional view of ascoma, asci, and ascospores of the teleomorph. D-F, sectional view of conidioma, conidiogenous cells with developing conidia, and mature conidia.

tissue, thus being entirely immersed and causing a few hump-like elevations in the central blackened tissue. The fructifications are covered above by a very thick clypeus. The ascomata have a fleshy light coloured peridium and bear more or less clavate, unitunicate asci with non-amyloid apical apparatus and intermixed with hyaline, septate paraphyses. The ascospores are more or less ovoid, unicellular, and hyaline to subhyaline. The anatomical details of the conidiomata are similar to those of the ascomata (Fig. 12.5A,D) except that the walls are thicker and more stromatic, the clypeus is thicker, and the conidial hymenium arises all around the cavity of the irregularly loculate conidioma. The conidiogenous cells are subcylindrical to irregular, hyaline to subhyaline, and bear fusiform, ellipsoidal, hyaline to subhyaline conidia with a more or less truncate base and one or two simple or irregularly branched appendages at the apex. The conidiogenous cells occasionally proliferate percurrently. After a study of the slides of *Ciliochora longiseta* available in the Höhnel herbarium in FH, I am led to conclude that the fungus from the Philippines in BPI is conspecific with *Ciliochora longiseta*. The Ascomycete associated with it is identified as an undetermined species of *Phyllachora* in the Polystigmataceae (Sphaeriales). Many species of *Phyllachora* have been described with anamorphs which appear to be in reality the spermatial states of the fungus. The presumptive relationship between *Ciliochora longiseta* and the *Phyllachora* sp. is inferred here by virtue of the architectural similarity of the conidiomata and the ascomata, which are also found closely associated in nature.

*CRYPTOSPORIOPSIS** (COELOMYCETES) AND *MELCHIORA** (SPHAERIALES).

This *Cryptosporiopsis-Melchiora* connection is yet another example of presumptive relationship based on evidence of architectural similarities between the conidiomata and ascomata, and intimate association of the two states. These states are present in a collection of leaves of *Bambusa* sp. from South India, the sporomata of both states developing in linear, crustlike stromata disposed parallel to the veins and midrib. In longitudinal section, the stromata appear to be composed of up to 5 locules, with the thick outer walls composed of pseudoparenchymatous tissue made up of isodiametric, thick-walled cells, and the inner separating walls between the locules being composed of columnar cells (Figs. 12.6A,B). Each locule has an ostiole and the sporomata are glabrous. The asci are unitunicate, cylindrical to clavate, hyaline and thin-walled with a non-amyloid apical apparatus. Paraphyses are absent. The ascospores are more or less fusiform to fusiform-elliptic, 1-septate with the wall often constricted at the septum, hyaline and smooth-walled. The conidiophores arising all around the cavity of the locules of the conidiomata are septate, branched, hyaline and terminate in phialides. The conidia are fusiform-elliptic or slightly irregular in shape, unicellular, hyaline. In view of the striking structural similarities between the closely associated conidiomata and ascomata, there seems to be little doubt that the two states are connected. The teleomorphs previously recognized for *Cryptosporiopsis* are species of *Pezicula, Ocellaria* and *Habrocystis*, all of which belong in the Dermateaceae (Helotiales).

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* Provisional identifications only. Detailed taxonomic and nomenclatural accounts of these taxa will be published elsewhere.

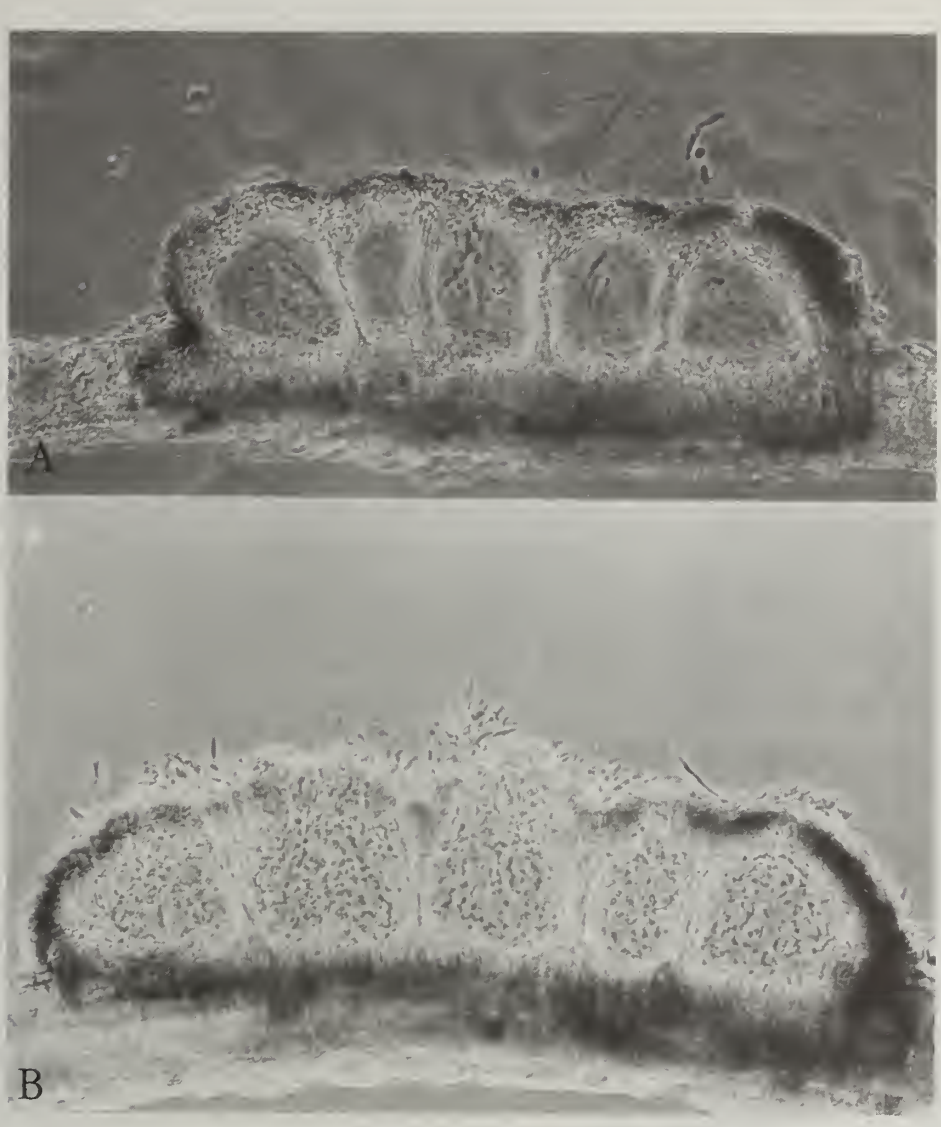


Fig. 12.6 *Melchioria* sp. and *Cryptosporiopsis* sp. A, longitudinal section of an ascoma. B, longitudinal section of a conidioma.

COMA CIRCULARIS (COELOMYCETES) AND *RHOPOGRAPHUS* (STIGMATEACEAE).

In an account of *Coma circularis*, Nag Raj & Kendrick (1972) reported the occurrence of a microconidial state associated with the Coelomycete. A re-examination of the original specimen has revealed the presence of an Ascomycete in intimate association with the two anamorphs (Fig. 12.7A-D). The ascomata are scattered to gregarious, stromatic, immersed, later erumpent, irregularly loculate, with slightly papillate ostioles. The asci are bitunicate, hyaline and octosporous. The ascospores are scolecosporous, 3-septate, at first hyaline, thin-walled and smooth, but ultimately pale brown to brown, thick-walled, and verruculose with a tendency for the individual ascospore cells to separate at the septa. The fungus has provisionally been identified as a species of *Rhopographus* Nits. *Montagnella eucalypti* Cke. and *M. rugulosa* Cke., both with 3-septate, coloured, scolecosporous ascospores have been reported on leaves of *Eucalyptus* spp. The status of *Montagnella*, however, appears to be in doubt, since the type specimen of *M. curcumamuel* Speg. has not been appraised, and there is a possibility that the original description of ascospores ("2-celled") referred to immature ascospores. Arx & Müller (1975) have suggested the reintroduction of the genus name *Gillotia* for species of *Montagnella* with 3-septate ascospores. Species of *Gillotia* also have an *Asteromella*-like spermatial (? microconidial) state. The points of significance as far as the material of *Coma circularis* is concerned, are that the ascomata of *Rhopographus* (or *? Montagnella/Gillotia*) are intimately associated with the conidiomata of the anamorph; the ascospores develop the same kind of thick walls, pigmentation and ornamentation as do the conidia. These features suggest a genetic connection between the two states.

ANAMORPHS OF SOME SPECIES OF *PHACIDIUM*.

The type specimen of *Coleophoma taxi* (Petr.) Nag Raj (≡ *Xenodomus taxi* Petr.), on needles of *Taxus brevifolia* from Idaho, also bears two other fungi. One of these is a Coelomycete possessing stromatic, irregularly loculate pycnidial conidiomata with an ostiole surrounded by a pseudoparenchymatous tissue darker than the walls, blastic-annellidic conidiogenous cells arising all round the cavity of the locules, and more or less reniform or lunate, unicellular, hyaline conidia bearing an irregular or funnel-shaped mucoid appendage at the apex. The other is a species of *Phacidium* with black ascomata; thin-walled, subcylindrical, unitunicate asci; filiform, septate paraphyses; and naviculate, unicellular ascospores. The conidiomata and ascomata often occur side by side (Fig. 12.8A). According to published literature, *Phacidium taxicolum* Dearn. & House can cause snow-blight of *Taxus* spp. DAOM has several collections disposed under this name, the hosts involved being *T. brevifolia* from British Columbia and *T. canadensis* from various localities in eastern U.S.A. and Canada. The collection on *T. brevifolia* from B.C. carried both the anamorph and teleomorph matching those found on the same host from Idaho. On the other hand, the collections on *T. canadensis* revealed the presence of another species of *Phacidium* and a Coelomycete (Fig. 12.8B) which had the same gross morphology as the Coelomycete occurring on *T. brevifolia* except for the fusiform conidia with phialidic conidium ontogeny, and significant quantitative differences. In all these collections the anamorphs and teleomorphs developed together. During the Peck foray in 1976, a collection of fallen leaves of *Gaultheria procumbens* was found to bear a species of *Phacidium* and a Coelomycete that was subsequently indentified as *Ceuthospora lunata* Shear. Conidial and ascosporic

Fig. 12.7 *Rhopographus* sp. and *Coma circularis*. A-C, sectional view of an ascoma, asci and partial view of ascospores of the teleomorph. D, conidium of the anamorph.

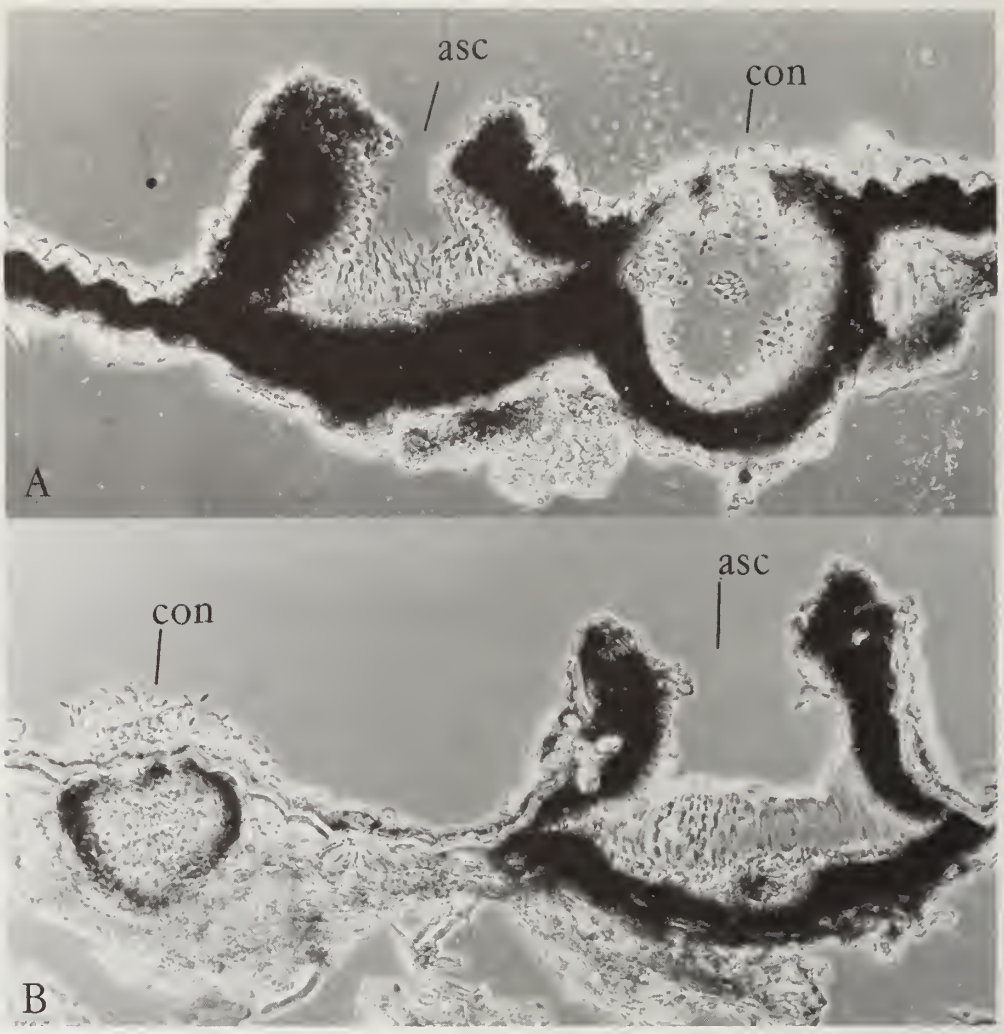


Fig. 12.8 *Phacidium* spp. and related anamorphs on *Taxus* spp. A, sectional view of an ascoma (asc) of *Phacidium* sp., and of a conidioma (con) of the anamorph, occurring on *Taxus brevifolia*. B, sectional view of an ascoma of *Phacidium taxicolum*, and of a conidioma of the anamorph, occurring on *Taxus canadensis*.

isolates yielded cultures of similar appearance and growth pattern on synthetic agar media. Both types of isolates produced abundant sclerotioid bodies on such media and on sterile plant substrates but failed to sporulate during the first two to three months, even after exposure to UV light. However, examination of a 10-month-old culture of an ascosporic isolate revealed conidium production, with the conidia matching those found in nature. This apparent genetic connection between the anamorph and teleomorph occurring on *Gaultheria procumbens* indicates that the two states occurring on *Taxus* may also be related. Consistent occurrence of the two states in close association, and occurrence of both on the same host species growing in separate geographic areas also support the probability of relationship. Species of *Phacidium* are known to have anamorphs in the form-genus *Ceuthospora*, which is characterized by black, immersed, pseudostromatic conidiomata with several separate locules, each locule opening by a furfuraceous ostiole; branched, septate, hyaline phialophores; and cylindrical, unicellular, hyaline phialoconidia with an apical mucoid appendage. The anamorphs occurring with species of *Phacidium* on *Taxus* spp. and *Gaultheria* differ from species of *Ceuthospora* and belong in an undescribed form-genus. The family Phacidiaceae is poorly defined, the taxonomy of the group remaining extremely confused. From the information available, it appears that a study of anamorphs, when these are present, may yield additional characters that would help in resolving the taxonomy of the Phacidiaceae.

FIBULOCOELA INDICA, A COELOMYCETE WITH BASIDIOMYCETOUS AFFINITIES.

In the latter half of 1970, I isolated a fungus in pure culture from leaf washings of dead, fallen leaves of *Bambusa* sp. lying on the ground. Later the cultures were grown on steam-sterilized leaves of sugarcane, but due to some unavoidable circumstances, all viable cultures of the fungus were lost, making extended studies impossible. Examination of the dried cultures showed some interesting features of the fungus, which are illustrated in Fig. 12.9A-C. The aerial mycelium is composed of branched, septate hyphae bearing clamp connections. Sections of the leaves revealed the presence of immersed, subepidermal, irregularly loculate pycnidial conidiomata with pseudoparenchymatous walls, but lacking ostioles. The conidial hymenium arising all round the cavity of the locules was composed of densely packed, septate, branched, hyaline conidiophores bearing clamp connections at the septa. The conidiogenous cells were more or less cylindrical, hyaline, thin-walled and gave rise to a single, terminal, holoblastic conidium. New conidiophores or conidiogenous cells originated from the clamp connections along the older conidiophores. The cigar-shaped, unicellular, hyaline conidia had a single, filiform, flexuous, apical appendage.

Among the Basidiomycetes, *Craterocolla* Bref., a member of the Tremellaceae, is the only genus known to have an anamorph producing conidia in gelatinous 'pycnidia', and disposed in the form-genus *Ditangium* Karst. According to Donk (1966), *Dacrymyces conglobatus* Peck is congeneric with *Ditangium*. The conidiomata of this fungus are gelatinous, cupulate, the walls being composed of plectenchymatous aggregations of branched, septate hyphae that do not bear any clamp connections. The conidial hymenium occurs in the concavity of the conidioma and is composed of numerous, irregularly branched, septate, hyaline conidiophores with integrated conidiogenous cells, each conidiogenous cell producing a cluster of holoblastic, lunate, unicellular, hyaline conidia. The term 'pycnidia' for the conidiomata of this fungus is inappro-

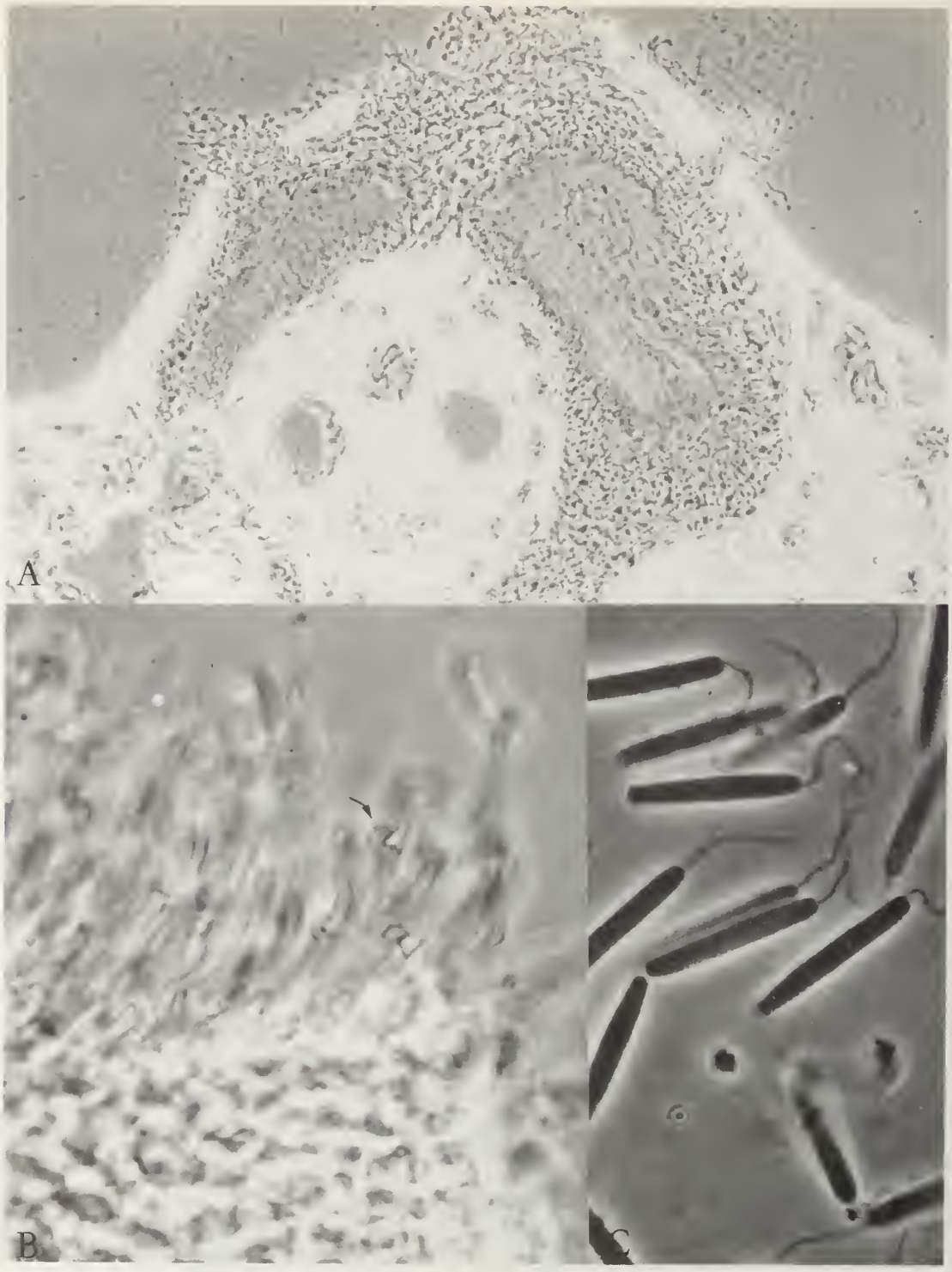


Fig. 12.9 *Fibulocoela indica:* a coelomycetous anamorph with basidiomycetous affinities. A-C, sectional view of conidioma, conidiophores bearing clamp connections (one clamp indicated by arrow), and mature appendage-bearing conidia.

priate. In view of a lack of information concerning the teleomorph of the Coelomycete on *Bambusa* sp., it is not possible to indicate its true affinities in the scheme of classification for the Basidiomycetes. However, I have disposed this unique anamorph in a new form-genus, *Fibulocoela* (Nag Raj 1978).

CONCLUSIONS

From the foregoing accounts, it can be seen that the four kinds of evidence can offer valuable clues to relationships between anamorphs and teleomorphs; the fact that, in one instance, relationship inferred from a close association of the two states (e.g., *Phacidium* sp. and a Coelomycete on *Gaultheria)* was confirmed by cultural evidence, indicates that such associations observed in nature cannot be ignored completely, but should be recorded. We have numerous reports of such presumptive connections in early mycological literature; unfortunately, with many such reports the documentation is not adequate or reliable enough to rule out the possibility of misdeterminations. One way of correcting this situation is to publish good illustrations of the taxa involved. Such an approach to documentation in the future will offer us better clues to the relationships between anamorphs and teleomorphs.

DIALOGUE FOLLOWING DR. NAG RAJ'S PAPER

VON ARX: What do you think about the taxonomic position of *Cryptosporella?*

NAG RAJ: I have not made a critical study of the type species. I have relied on keys in 'The Fungi' Volume 4A for my identifications.

VON ARX: I have studied the type and other species, but I have never seen the ring in the ascus tip which is supposed to be so conspicuous. There are many genera with asci similar to those you have illustrated -- *Ophiovalsa, Calospora, Calosporella* and *Hapalocystis.* All have rather thick-walled asci without refractive apical rings.

DE HOOG: I have the impression that intercalary conidiogenous cells may be useful in distinguishing certain groups. I have gathered from Dr. Hennebert that they were associated particularly with the Hemiphacidiaceae. Have you found any such associations?

VON ARX: Such conidiogenous cells, one above the other, are very common in coelomycetous anamorphs of discomycetes -- *Cryptocline, Cryptosporiopsis,* the anamorph of *Ophiovalsa,* and many others. Among the Hyphomycetes I can only think of *Sesquicillium.*

WEBSTER: Can't you confirm some of the connections you report by inoculating the host with ascospores and seeing if conidia develop?

NAG RAJ: I must remind you that in many cases, the material I worked with has been lying in a herbarium for a century or more. If I had fresh material I could do culture studies and be more sure of my results. The work I have reported on here is in fact, only incidental to my main purpose, which is to make monographic studies of some of the coelomycete genera.

MADELIN: Clearly, since fungi differ so widely in their life cycles, nutritional and ecological requirements, we will not be able to set up any single prescribed set of rules like Koch's postulates to determine whether a connection is genuine. I wonder if the answer, at least for the time being, might be to have a series of adjectives that could describe the kind of evidence one has. Perhaps 'Associative', and 'Cultural' would help.

KENDRICK: We were planning to give a code symbol with each of our listings, to indicate this very thing.

LUTTRELL: That might not help much, because even a cultural connection is no better than the manner in which it is established. As Dr. Von Arx said earlier, some connections may simply be contaminants.

KENDRICK: That is true and, to look at the other end of the scale, some of the 'associative' connections Dr. Nag Raj has made are extremely convincing, especially when the associated anamorph and teleomorph apparently share a rather unusual kind of architecture. Of course, that might be an example of what Dr. Luttrell pointed out earlier -- conidia and asci being formed successively in the same fructification.

WEBSTER: It might also be a result of the particular host reaction forcing a similar morphology on any fungus that attacks it: you must be very careful in interpreting these architectural similarities. But you must also document the evidence you have, so that others may build on it.

VON ARX: I'd just like to comment on the magnitude of the problem facing students of the Coelomycetes. We know that one species, *Phoma exigua*, has had about 1,000 names applied to it. We know that the anamorph of *Botryosphaeria quercuum* has more than 400 names. When I was revising *Colletotrichum*, I found about 10 generic synonyms, and for the anamorph of *Glomerella cingulata* I found about 800 synonyms. Many, many genera of Coelomycetes need revision. Many of them now contain large numbers of species. It is very important that this work be done, because some of these genera are vital to phytopathologists, who often have to work with absolutely wrong names when they deal with Coelomycetes. Dr. Nag Raj deserves every support and encouragement in his excellent revisionary and monographic studies.

The next chapter offers a very broad survey of anamorph-teleomorph relationships in the Ascomycetes, and focuses on some genera which seem intermediate in condition between unitunicate and bitunicate. Having thrown out this challenge to the generally accepted dichotomy in the Ascomycete classification, Dr. von Arx proposes and presents a much-simplified scheme that incorporates anamorphic data.....

13
Ascomycetes as Fungi Imperfecti

J.A. Von Arx

Many Ascomycetes have conidial states. When we culture an Ascomycete, it may form only the teleomorph, only the anamorph, or both states. A comparative study of the Ascomycetes without a simultaneous study of their respective anamorphs would be inadequate. The anamorphs must be considered in the classification of the Ascomycetes. The possession of similar anamorphs is generally a reliable indicator of relationship within the Ascomycetes.

All existing systems of the Fungi Imperfecti have no phylogenetic, but marked practical, value. The best system is that which is most useful for identification purposes. With an as yet hypothetical system based on conidiogenesis, it is still impossible to elaborate natural taxa. Many genera, even as circumscribed in the most recent text books, are unnatural. A phylogenetically satisfactory classification of the Fungi Imperfecti can be based only on the system of the Ascomycetes. A student of the Fungi Imperfecti should, therefore, simultaneously compare their teleomorphs.

Some ascomycete genera are mainly based on properties of anamorphs. The voluminous genus *Sclerotinia* has been subdivided into a number of segregate genera such as *Botryotinia*, *Gloeotinia*, *Monilinia* or *Septotinia*, on the basis of anamorphs belonging to the form genera *Botrytis*, *Endoconidium*, *Monilia* and *Septotis*, respectively. Some *Sclerotinia* species, however, have no conidial state or include only spermatial states, and it may be for this reason that the above classification has only been accepted with hesitation. All these genera are, without doubt, close to each other (von Arx 1974).

A different case is the genus *Ceratocystis*, in which many unrelated species have been classified. We now restrict *Ceratocystis* to species with phialidic anamorphs of the genus *Chalara*. The species with *Sporothrix*, *Graphium* or similar states forming blastic-sympodial conidia must be classified in a separate genus, for which the name *Ophiostoma* is available. The position of this genus is problematic, because the cells contain rhamnose and a trace of cellulose, both of which are absent in *Ceratocystis* and in all other Ascomycetes, as far as we know. The teleomorphs *Ceratocystis* and *Ophiostoma* are morphologically similar but, judging from chemical data and the anamorphs, the two holomorphic genera are not closely related (Weijman & de Hoog 1975). *Ceratocystis* may be close to *Chaetosphaeria* (Sphaeriaceae), since both at least have similar phialidic anamorphs *(Chalara, Chloridium, Gonytrichum)*.

The families Melanosporaceae, Sordariaceae, Hypocreaceae, Sphaeriaceae, Polystigmataceae, Diaporthaceae, Hypomycetaceae and Clavicipitaceae of the Sphaeriales (all sensu von Arx 1976)

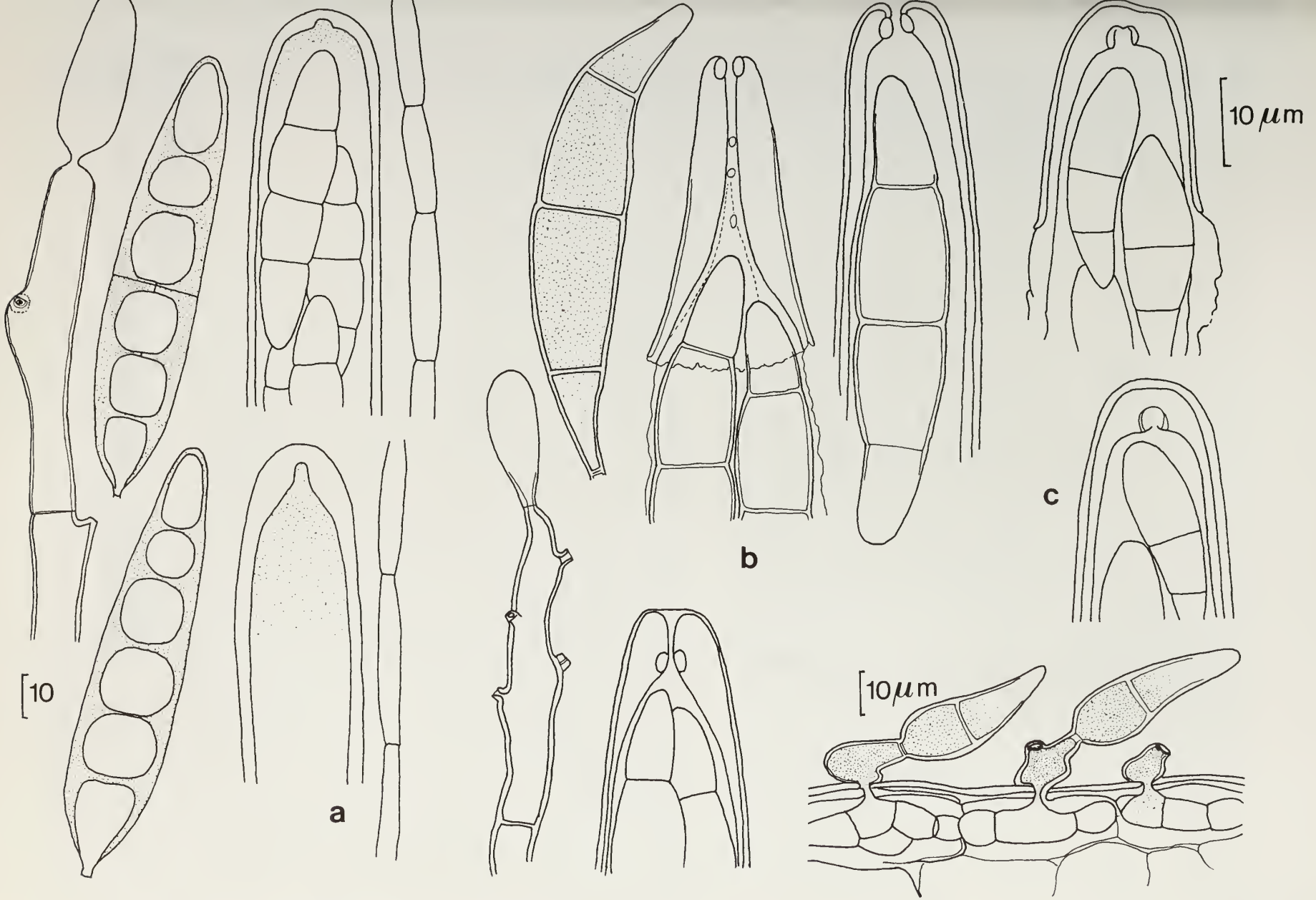


Fig. 13.1 A, *Setosphaeria turcica*, apical parts of asci with ascospores and paraphyses, and the *Exserohilum* anamorph. B, *Magnaporthe salvinii*, apical parts of asci with ascospores, and the *Nakataea* anamorph. C, *Buergenerula caricis*, apical parts of asci with ascospores, and the (unnamed) anamorph.

comprise most of the unitunicate Pyrenomycetes. They are close to each other, and many intermediate forms exist between mainly the Sphaeriaceae, Hypocreaceae and Polystigmataceae. Many species have phialidic anamorphs forming wet (rarely dry) masses of usually hyaline conidia (e.g., the form genera *Acremonium, Phialophora, Verticillium, Fusarium, Cylindrocarpon, Sphacelia, Colletotrichum, Discula, Phomopsis).* Additional, usually chlamydospore-like, anamorphs may also be formed (e.g., *Botryotrichum, Sepedonium* or *Monilia*; this last being known in some *Neurospora* species).

Similar phialidic anamorphs are known in the Helotiales and Phacidiales, and these groups must be regarded as the apothecia-forming counterparts of the above-mentioned families of the Sphaeriales (von Arx 1974, 1976).

In the Xylariaceae, which incorporate genera such as *Xylaria, Hypoxylon, Rosellinia* and *Ascotricha,* the conidia are pigmented, have a broad, truncate base and are formed sympodially. These anamorphs belong to form genera such as *Nodulisporium* and *Dicyma*, and indicate that the Xylariaceae occupy a rather isolated position.

In many Microascaceae, the broad-based conidia are usually also pigmented, but develop on percurrent conidiogenous cells in basipetal chains (form genera *Scopulariopsis* and *Cephalotrichum*). In other species, however, the conidiogenous cells are phialide-like.

Within the cleistocarpous Ascomycetes generally treated as Eurotiales, whole families have been based on conidial anamorphs. The Onygenaceae and Gymnoascaceae are restricted to genera with arthric or aleuric anamorphs such as *Chrysosporium* or *Malbranchea*, or without an anamorph. The Eurotiaceae contain only genera with phialidic anamorphs forming conidia in 'true' chains (Subramanian 1972) such as *Penicillium, Aspergillus* or *Paecilomyces.* These anamorphs suggest a relationship to other phialidic fungi, e.g., the Hypocreaceae, as pointed out by Malloch & Cain (1972) and others. The genus *Sphaeronaemella* with its *Gabarnaudia* anamorph may be intermediate between the Eurotiaceae and Hypocreaceae. On the other hand, several Ascomycetes are known whose classification in either the Eurotiaceae or Onygenaceae is uncertain.

The Ascomycetes are usually subdivided into Eu-Ascomycetes with unitunicate asci and Loculo-Ascomycetes with bitunicate asci. The two groups are considered to represent two phylogenetic lines without intermediate forms. The only taxonomist who never accepted this supposition was Franz Petrak in Vienna. He often described intermediates between the unitunicate Sphaeriales and the bitunicate Dothideales. In most cases it is easy to determine the uni- or bi-tunicate nature of the ascus, but I have experienced some difficulty when studying species described as intermediates by Petrak. The results of this study will here be discussed by means of two examples.

The first concerns *Setosphaeria, Magnaporthe* and *Buergenerula,* three genera with species parasitic on graminaceous plants and with dematiaceous anamorphs (Fig. 13.1). The genus *Setosphaeria* has *Exserohilum* conidia and is placed in the bitunicate Pleosporaceae by Leonard & Suggs (1974). *Magnaporthe* has a *Nakataea* anamorph and is classified by Krause & Webster (1972) in the unitunicate Diaporthaceae, because the asci have an apical refractive ring. *Buergenerula caricis,* a species placed in the Pleosporaceae by Müller (1950), and in the Physosporellaceae (unitunicate Pyrenomycetes) by Barr (1976), has an unnamed anamorph close to *Curvularia* (von Arx 1977). These anamorphs are similar and indicate a close relationship between the three ascomycete genera, as do the structure of the ascomata and other characters.

Their classification in the Pleosporaceae should be preferred, because other closely related genera are *Pleospora* with *Stemphylium* anamorphs, *Cochliobolus* with *Curvularia* or *Bipolaris* conidia, and *Pyrenophora* with *Drechslera* conidia. The genus *Drechslera* sensu Ellis (1971) is heterogeneous and should be reconsidered in the sense of Luttrell (1977). *Bipolaris* can hardly be distinguished from *Curvularia*. The genus *Pyricularia* is also close to *Nakataea* and *Curvularia*. Its teleomorph has been classified in the imperfectly known genus *Ceratosphaeria* of the Diaporthaceae by Hebert (1976), but *Magnaporthe* would probably be a better name for it.

In all the ascomycete genera just mentioned, the asci are bitunicate, although they frequently do not function as such because the ascospores are not violently discharged, but extruded in a slimy mass.

The second example comprises ascomycete genera partly classified in the Diaporthaceae and Amphisphaeriaceae, partly in the Pleosporaceae (Massariaceae); all with acervular or pycnidial anamorphs and pigmented conidia with a broad, truncate base. All the fungi studied develop saprophytically in bark, and form immersed, often stromatic, ascomata with erumpent ostioles which are usually lined with periphyses. In all these genera the asci have rather thick, probably bitunicate walls; the apices, however, often include thickenings, caps or rings.

In *Diaporthe*, the type genus of the Diaporthaceae, and in many other genera of the family, the asci are clavate-fusiform, thin-walled, with a single refractive ring in the apex (Fig. 13.2 A). The ascomata are usually rather large, thick-walled, pseudoparenchymatous, with an often elongate ostiolar beak lined with periphyses. The often fusiform ascospores are not violently discharged but are liberated in a slimy mass and usually remain attached to the apical ring by slimy fibrils. Many Diaporthaceae include phialidic anamorphs producing pycnidial conidiomata, e.g., *Phomopsis*. In *Sydowiella fenestrans* the asci are cylindrical, surrounded by a few paraphyses (Fig. 13.2 B), and the species has no anamorph.

In typical species of the genus *Melanconis*, e.g., *M. stilbostoma*, the apical structure of the asci is more complicated, two non-refractive rings and a cap being visible (Fig. 13.3 A). Paraphyses are usually absent. The ascospores become free after dehiscence of the outer ascus wall at its apical part. This has been defined as "pseudo-jack-in-the-box" by Chadefaud (1973). In the *Melanconium* anamorph the pigmented conidia have a truncate base and develop singly on often percurrent conidiogenous cells. In *Massariovalsa* the asci have a rather similar apical structure, but have a thicker wall and are surrounded by numerous paraphyses (Fig. 13.3 B). The structure of the stromata and the ascoma wall is like that in *Massaria*, and the anamorph is pycnidial with large, pigmented conidia. *Melanconis* and *Massariovalsa* are related (Wehmeyer 1941 united them), but their relationship to *Diaporthe* is uncertain. These genera are probably closer to some Amphisphaeriaceae, such as *Discostroma*, which also have pigmented (but septate) conidia with truncate bases (*Sporocadus*, *Seimatosporium*). In *Discostroma* (syn. *Griphosphaeria*), parts of the apical structure of the thin-walled asci are amyloid. In the closely related genera *Broomella* and *Lepteutypa* (with *Pestalotia* anamorphs) often no amyloid reaction, or only a weak one, could be observed.

Pseudovalsa and *Prosthecium* species, hitherto classified in the Diaporthaceae, have thick-walled, apparently bitunicate asci with an apical, annellated cone (Fig. 13.4 B,C,D). The *Coryneum* and *Stilbospora* anamorphs are acervular or (rarely) pycnidial, with many-celled, often distoseptate, pigmented conidia, formed singly and with a truncate base, on often

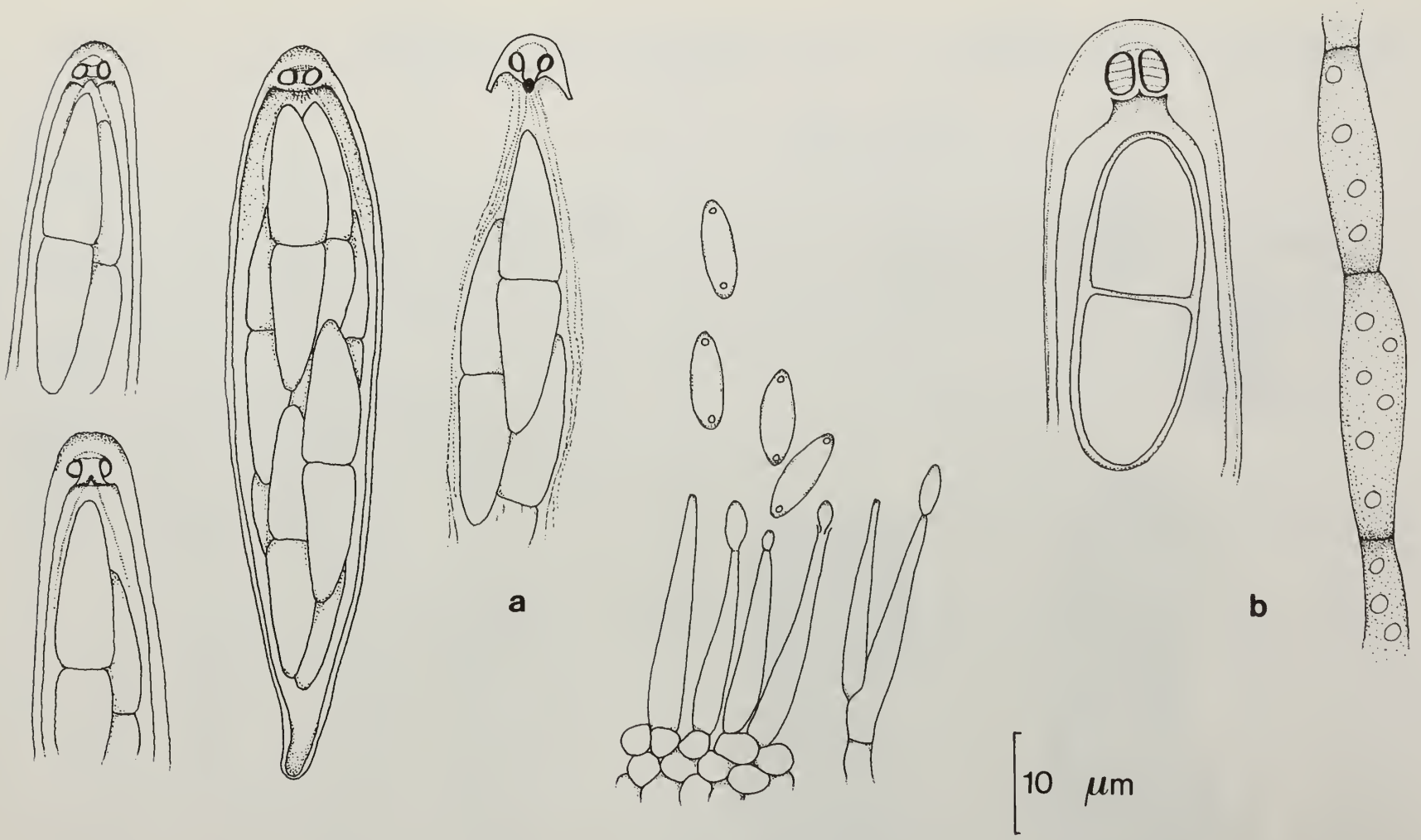


Fig. 13.2 A, *Diaporthe leiphaemia*, asci with ascospores, and the *Phomopsis* anamorph. B, *Sydowiella fenestrans*, apical part of an ascus with an ascospore and part of a paraphysis.

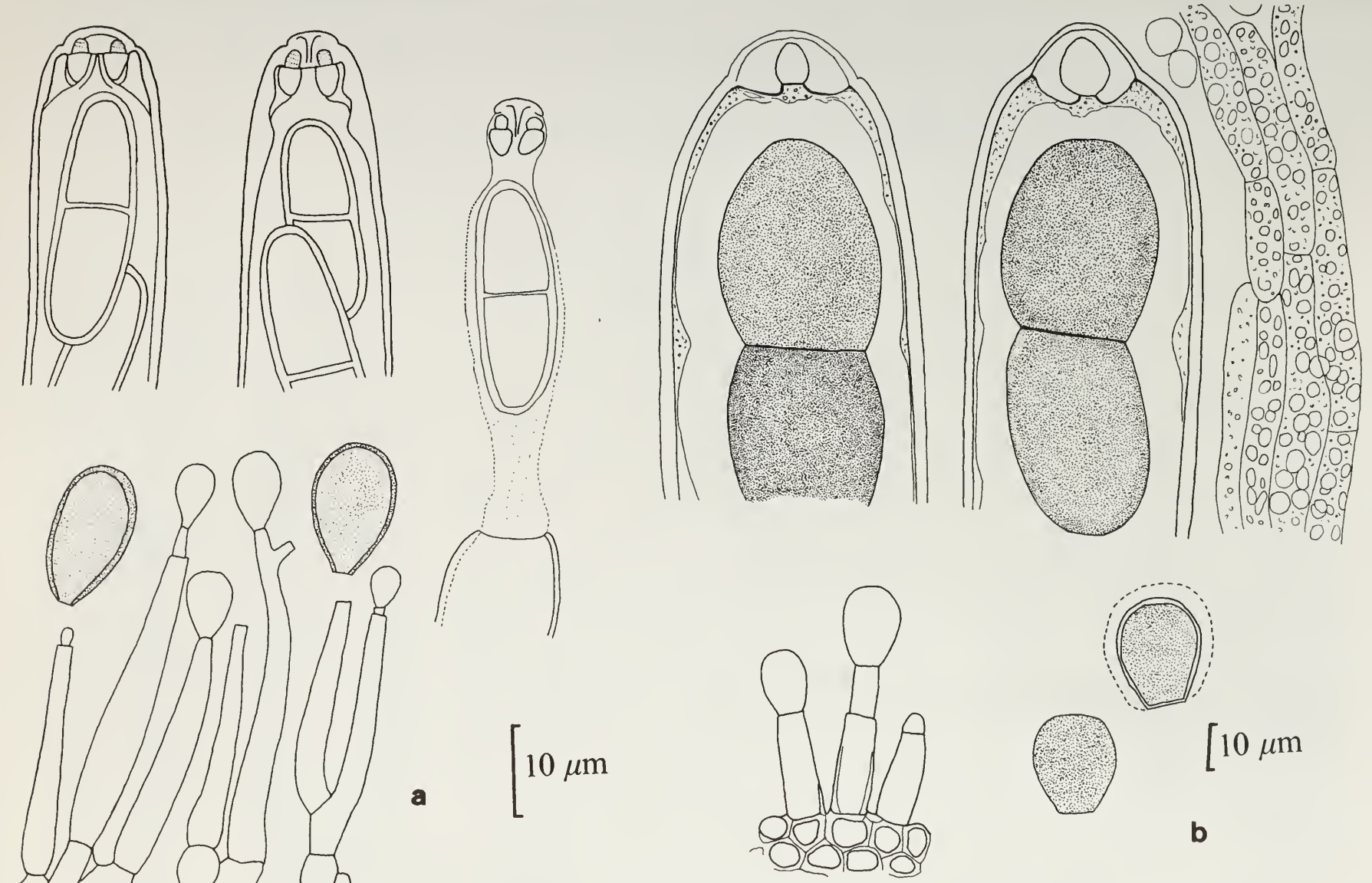


Fig. 13.3 A, *Melanconis stilbostoma*, apical parts of asci, and the *Melanconium* anamorph. B, *Massariovalsa sudans*, apical parts of asci with ascospores and paraphyses, and the *Melanconiopsis* anamorph.

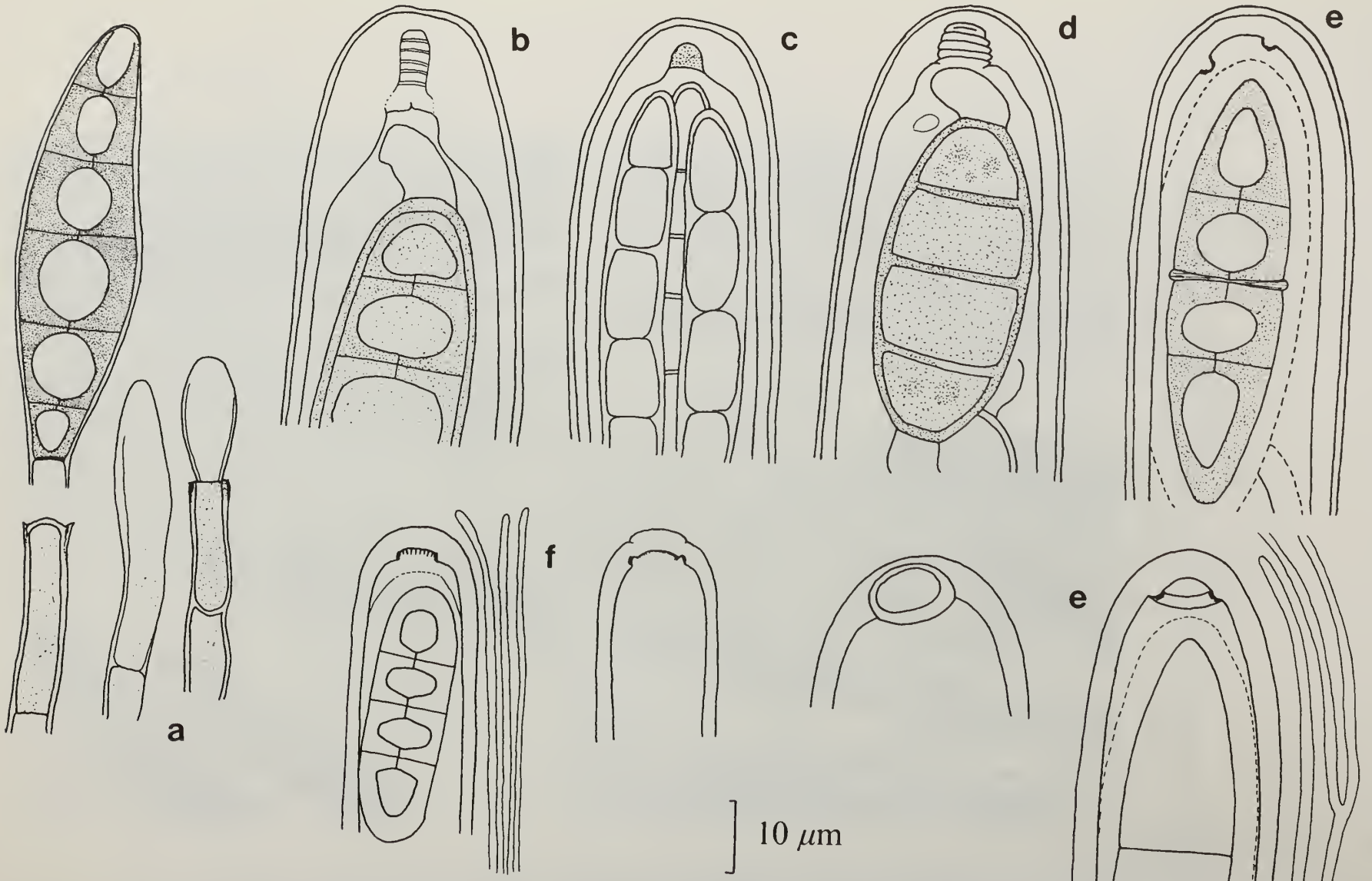


Fig. 13.4 A, *Coryneum* sp. conidiogenous cells and a conidium; B, *Pseudovalsa lanciformis*; C, *Pseudovalsa longipes*; D, *Prosthecium ellipsoideum*; E, *Massaria inquinans*; F, *Massaria (Aglaospora) profusa*, apical parts of asci, some with ascospores and paraphyses.

Fig. 13.5 A,B, *Massaria inquinans* Ces. & de Not. C,D, *Massaria profusa* (Fr.) Petr. (=*Aglaospora profusa* (Fr.) Ces. & de Not.), asci with an apical ring, ascospores and paraphyses. ca. x700

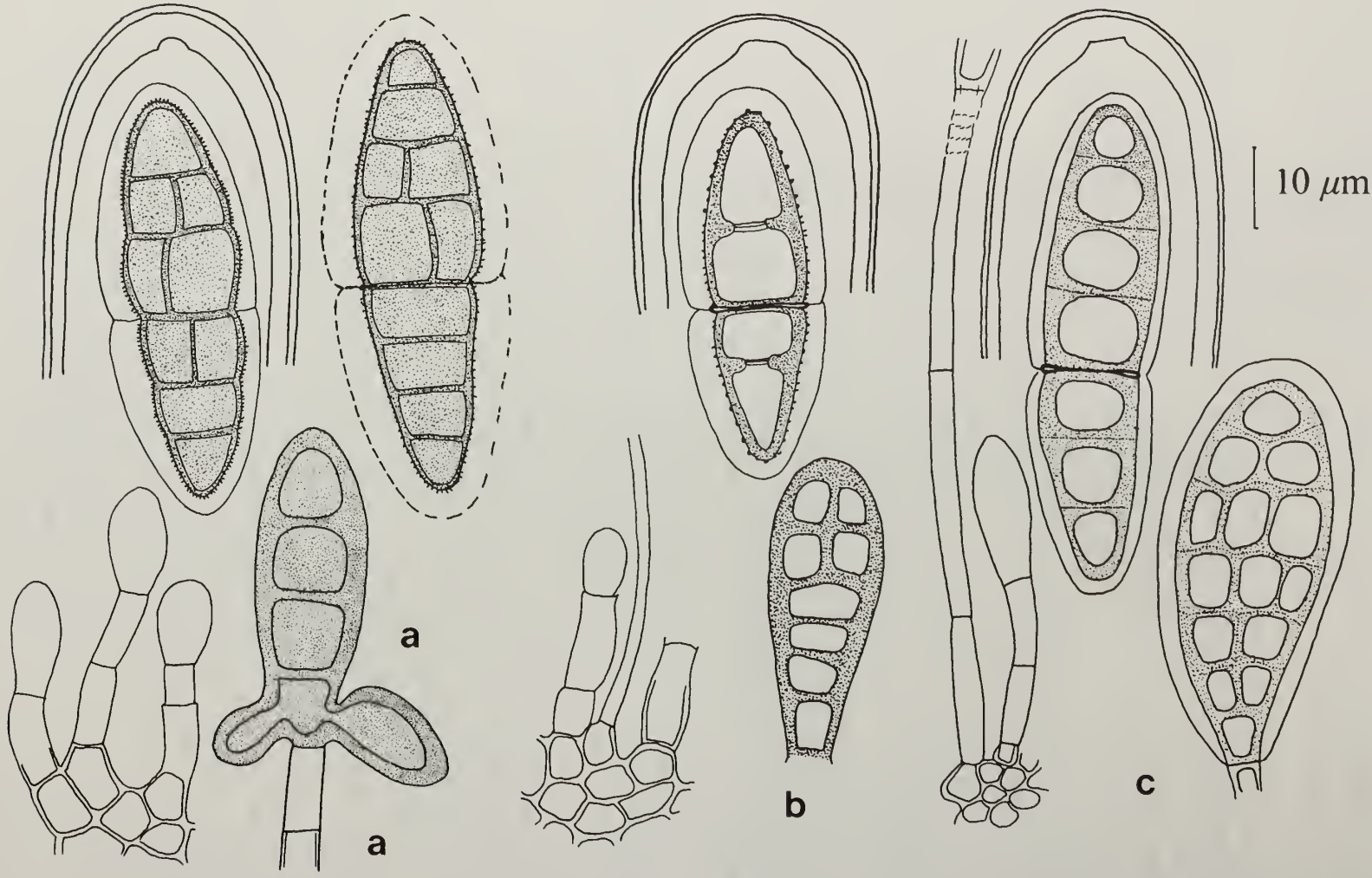


Fig. 13.6 A, *Pleomassaria siparia*, apical part of an ascus, ascospores, and the *Prosthemium* anamorph. B, *Splanchnonema (Stigmatomassaria) pupula*, apical part of ascus, ascospore, and *Steganosporium* anamorph. C, *Splanchnonema (Massaria) argus*, apical part of ascus, ascospore, and *Steganosporium (Myxocyclus)* anamorph.

percurrent conidiogenous cells (Fig. 13.4 A). In *Pseudovalsa disciformis*, the ascospores are pigmented and distoseptate; other species have hyaline or only slightly pigmented, 2- or many-celled ascospores without thickened inner walls (Wehmeyer 1941).

The genus *Aglaospora* has been reintroduced by Wehmeyer (1941) and by Shoemaker & Le Clair (1975). The two species *A. profusa* and *A. effusa* had been classified in *Pseudovalsa* by Winter (1887), and in *Massaria* by Petrak (1923). The latter was correct because *A. profusa* (Fig. 13.5 C,D) and *M. inquinans* (Fig. 13.5 A,B), the type species of their respective genera, are similar in that the asci are thick-walled, have a broad apical ring, and are surrounded by numerous filiform paraphyses and, further, in that the ascospores are 4-celled, distoseptate, with a thickened median septum (Fig. 13.4 E,F). The structure of the ascomata and the hymenial layer, with numerous paraphyses and periphyses, is similar to that of *Massariovalsa sudans* (Fig. 13.3 B). Connections to anamorphs have not been established in *Massaria*.

In *Splanchnonema* and similar genera, hitherto often combined with *Massaria* and recently reintroduced by Shoemaker & Le Clair (1975), the asci are clavate, thick-walled, bitunicate, lack apical rings (Fig. 13.6) and are surrounded by numerous filiform paraphyses. The ostiolar pore of the thick-walled ascomata is not lined with periphyses. The ascospores are obovate or elongate pyriform, attenuated towards the base, 2- or many-celled pigmented, and eu- or disto-septate. However a tropical, as yet probably undescribed, species has ellipsoidal-fusiform, 4-celled ascospores, similar to those of *Massaria*. The anamorphs of species of *Splanchnonema* and *Pleomassaria* belong to genera such as *Prosthemium, Steganosporium* and *Scolecosporium*, and are rather similar to the *Coryneum* anamorph of *Pseudovalsa*.

It may thus be concluded that *Pseudovalsa, Prosthecium* (and other genera of the Diaporthaceae) have apparently bitunicate asci, and show relationships to *Massaria* and *Splanchnonema* on the one hand, and to *Massariovalsa* and *Melanconis* on the other. Their anamorphs also indicate a close relationship. *Pseudovalsa, Prosthecium, Massaria, Splanchnonema, Pleomassaria, Massarina* and some other genera will have to be classified in a separate family, for which the name Massariaceae Winter is available. Are these fungi intermediates between Pleosporaceae and Diaporthaceae? If so, this would result in a simplification of the Ascomycete system, and the distinction between Eu- and Loculo-Ascomycetes would be superfluous.

The respective anamorphs can help us to construct a more simple and more natural system of the Ascomycetes. Von Arx & Müller (1975) classified all bitunicate Ascomycetes in one order, Dothideales, which would be linked to the unitunicate Sphaeriales by, for example, the genera discussed above.

The Acrospermataceae may be another group of fungi linking the Dothideales and the Sphaeriales. The genera *Acrospermum, Tubeufia, Podonectria* and *Oomyces* have recently been referred to the Pleosporaceae (Eriksson 1967, Pirozynski 1976), but many characters also show them to be close to the Clavicipitaceae and Hypomycetaceae of the Sphaeriales. This supposition can also be supported by the respective anamorphs (Webster 1956, Gams & Hoozemans 1970, Pirozynski 1972).

The Ascomycetes should be divided into only a few orders, e.g., the Dothideales, Sphaeriales, Helotiales, Pezizales, Tuberales, Erysiphales, Eurotiales and Gymnascales. Such a system would be more natural than the existing one which has 2 or 3 classes or subclasses and many orders, of which some are fairly natural, but most have proved to be very unnatural.

The following arrangement is therefore proposed.

A SYSTEM OF ASCOMYCETES, PARTLY BASED ON THEIR ANAMORPHS

Teleomorphs	Typical anamorphs
A. Gymnoascales	
1. Gymnoascaceae	arthric-aleuric: *Chrysosporium, Microsporon,*
2. Onygenaceae	*Trichophyton, Malbranchea.*
B. Eurotiales	
1. Eurotiaceae	phialidic, catenulate: *Penicillium, Aspergillus*
2. Pseudeurotiaceae	phialidic-sympodial: *Chalara, Acremonium.*
C. Sphaeriales	
1. Hypocreaceae	phialidic-sympodial: *Gabarnaudia, Gliocladium, Acremonium, Trichoderma, Fusarium, Cylindrocarpon*
2. Sphaeriaceae (incl. *Ceratocystis*)	phialidic: *Chloridium, Chalara, Monocillium, Fusarium*
3. Polystigmataceae	phialidic, coelomycetous: *Colletotrichum, Linochora*
4. Cryptosporellaceae	phialidic, pycnidial: *Disculina, Fusicoccum*
5. Diaporthaceae	phialidic: *Phomopsis, Discula, Phialophora*
6. Clavicipitaceae	phialidic-sympodial: *Sphacelia, Hirsutella*
7. Hypomycetaceae	phialidic-sympodial: *Cladobotryum, Sibirina*
8. Sordariaceae (incl. *Chaetomiaceae, Melanosporaceae, Coniochaetaceae, Coronophoraceae*)	phialidic: *Phialophora, Cladorrhinum*
9. Ophiostomataceae (excl. *Ceratocystis*)	sympodial: *Sporothrix, Verticicladiella, Graphium (Pesotum)*
10. Xylariaceae	sympodial, cicatr.: *Nodulisporium, Dicyma*
11. Amphisphaeriaceae (incl. *Melanconis*)	basipetal (percurrent) or sympodial: *Pestalotia, Sporocadus* (incl. *Stigmina*), *Seiridium, Seimatosporium, Melanconium*
12. Microascaceae	basipetal: *Scopulariopsis, Cephalotrichum*
D. Phacidiales	
1. Phacidiaceae	phialidic: *Ceuthospora, Rhabdogloeum, Titaeosporella*
2. Hypodermataceae	phialidic: *Melasmia, Leptostroma*
E. Helotiales	
1. Dermateaceae	phialidic or blastic (often rather broad-based or percurrent): *Marssonina, Phloeosporella, Cryptocline, Cryptosporiopsis*
2. Leotiaceae (Helotiaceae)	phialidic: *Phialophora, Brunchorstia, Hainesia*
3. Sclerotiniaceae	phialidic: *Myrioconium* (spermatial); blastic or acropetal-meristematic: *Botrytis, Monilia, Septotis, Endoconidium*

F. Pezizales

1. Pezizaceae.....blastic: *Oedocephalum, Dichobotrys, (Botrytis-like)*

G. Erysiphales

1. Erysiphaceae.....acropetal, meristematic: *Oidium*

H. Dothideales (all bitunicates)

1. Dothideaceae.....blastic (single or basipetal): *Dothichiza, Hormonema*
2. Botryosphaeriaceae.....blastic (single or basipetal, usually pycnidial): *Phyllosticta, Kabatia, Dothiorella, Botryodiplodia, Haplosporella, Hormonema*
3. Leptopeltidaceae.....blastic (single or basipetal, pycnidial): *Leptothyrium*
4. Asterinaceae.....blastic (pycnidial): *Asterostomella, Capnodiastrum*
5. Parodiellinaceae.....blastic (single or basipetal, hyphom.): (incl. Englerulaceae) *Mitteriella, Sarcinella, Clasterosporium, Septoidium*
6. Myriangiaceae.....phialidic or sympodial: *Sphaceloma*
7. Stigmateaceae.....blastic, sympodial or percurrent, truncate base, pigmented: *Fusicladium, Karakulinia, Spilocaea*
8. Mycosphaerellaceae.....1. sympodial (hyphom.): *Cercospora, Ramularia, Cladosporium*
   2. basipetal (pycnidial): *Phoma, Ascochyta, Septoria*
9. "Phaeosphaeriaceae".....blastic, basipetal (pycnidial): *Phoma,* (incl. Dimeriaceae) *Coniothyrium, Pyrenochaeta, Stagonospora, Hendersonia*
10. Pleosporaceae (s. str.).....blastic, sympodial, thick-walled, pigmented (hyphom.): *Alternaria, Stemphylium, Curvularia, Bipolaris, Drechslera, Exserohilum, Nakataea, Pyricularia*
11. Massariaceae.....blastic, single or percurrent, thick-walled (acervular): *Prosthemium, Steganosporium, Coryneum, Stilbospora*
12. Acrospermataceae(?).....blastic-sympodial (hyphom.): *Helicoma,* (incl. *Tubeufia*, etc.) *Helicosporium, Dactylella, Monacrosporium*

The Hemi-Ascomycetes (Endomycetales, Taphrinales) are excluded from the Ascomycetes proper.

Anamorphs are unknown in several families of the Dothideales, in the Amphisphaeriaceae of the Sphaeriales, in most of the Pezizales, and in the Tuberales. In a large number of genera, only a restricted number of species are known to include anamorphs. For this reason the

classification given above is only of limited value and is incomplete.

The term phialide is used in a limited sense; it is restricted to elongated, awl- or flask-shaped conidiogenous cells with or without collarettes. Forms with phialides are often close to those with sympodial conidiogenous cells. Genera such as *Beauveria*, *Isaria* or conidial *Pseudeurotium* are considered to have descended from phialidic forms. In *Chloridium* and other phialidic genera the conidia can also form sympodially. The broad conidiogenous cells known in many pycnidial genera such as *Phoma*, *Ascochyta*, *Septoria*, *Leptothryium*, *Kabatia* or *Phyllosticta* are not considered to be phialides, even when the conidia are basipetal. The terms "poroconidia" and "annellophores = annellides" are regarded as misleading and are therefore not used. In such cases conidiogenesis is termed blastic, The conidiogenous cells may elongate sympodially or percurrently, but intermediate forms exist, and the taxonomic value of this feature is negligible. Compare, in this regard, the closely related genera *Spilocaea*, *Fusicladium* and *Karakulinia* (*Cladosporium* pro parte).

The presence or absence of chlamydospores or of aleurioconidia (e.g., *Sepedonium*, *Mycogone* or *Botryotrichum*) is not considered.

After that rather iconoclastic talk (first delivered during IMC2, Tampa, the week before Kananaskis-II), which gave us yet another version of the classification of Ascomycetes to add to those we know already, it seemed appropriate to seek an objective way of testing these schemes. In the next chapter, Dr. De Hoog gives us a worked example of one such procedure by which he evaluates and compares two rather different schemes, both with phylogenetic implications. He includes test data from both anamorph and teleomorph, and concludes ... but you must read for yourself.....

14
Deductive Classification - Worked Examples Using Anamorph and Teleomorph Data in the Ascomycetes

G.S. De Hoog

INTRODUCTION

Nature is described by means of observations of events, which are in themselves unique (sense-data, Gilmour 1940) and only approximately reproducible. Once this information has been acquired, it must be arranged or ordered. Only the *knowledge* of nature can be ordered; so at this point we depart from Nature and proceed by working with secondary information only. Calling this ordering 'modelling of Nature' is, therefore, an overestimation of our abilities. The criteria by which Nature orders itself -- if it does so -- cannot be known, and thus the term 'Natural system' should be rejected as metaphysically meaningless. If we ignore the impossible demand to create such a 'natural system', we are limited only by: (a) the available data, (b) the criteria we use in the segregation of groups, and (c) the kind of system we aim to construct.

DATA

When constructing a system one cannot go beyond the immanent knowledge of the sense-data. Poor data will necessarily yield a bad or speculative system. One should therefore try to collect sense-data with a high information content. In addition, a basic scientific requirement is maximum reproducibility. Classical data (viz., those derived from intuitively selected characters) usually fulfill the first criterion, but can hardly be reproduced. The nominal data of numerical taxonomy (viz., those derived from all conceivable characters) are highly reproducible but often poorly chosen, neglecting the possible heuristic properties of the information.

SEGREGATION OF GROUPS

Two basically different kinds of segregation are possible. One can construct a hierarchical system of monothetic classes, each class differing from all others by having a set of diagnostic features shared by all the members of that class. This essentialistic approach is particularly common in classical taxonomy, and diagnostic features are still indispensable for the construction of identification keys. In practice, however, many taxa are not monothetic at all. If, for example, a single strain of *Leptodontium elatius* (Mangenot) de Hoog (1977) is observed on the natural substrate and in pure culture, a monothetic approach would result in the classification of this strain in two different genera, since they apparently do not share any diagnostic features. Their classification in the same genus makes this genus polythetic: dissimilar groups of organisms being united and connected by a taxon which resembles all

groups. No generic diagnostic features are then available. In such cases the system has not a hierarchical, but a reticulate structure. Classes are often not clearly delimited, but can be recognized only by relative discontinuities in the occurrence of certain character-states (Sneath 1976). Any grouping is then partly dependent on the choice of the specimens to be classified (de Hoog 1977), and adding new specimens changes the pre-achieved grouping (Jardine & Sibson 1968, Williams & Clifford 1971).

In conclusion, the construction of a hierarchical system is only possible if the groups are monothetic. If not, every abstraction of diagnostic features of lower taxa in order to construct higher taxa will cause some distortion, which grows exponentially with the number of steps. Numerical classification is suitable for polythetic groups, but not applicable to dissimilar taxa without severe character selection and artificial standardization. Hence, in every inductive classification, particularly in the construction of higher taxa, irreproducible distortions are unavoidable.

KINDS OF SYSTEMS

Systematization can be based on two very different concepts: structure or genesis. Emphasizing one at the expense of the other has led to the controversy between 'phenetic' and 'phyletic' taxonomists. There is, in fact, no logical need for either structure or genesis to be emphasized. In practice, however, we only have empirical information about structure (that is, including development); our information on genesis consisting of an empirical structural component plus a theoretical component. The phyletic aspects can be studied only if the theoretical considerations are stated explicitly, viz., by changing our criteria (b) and aims (c), and the structural component handled accordingly. Note that phyletic derivation without a fossil record is not unwarranted, as Hull (1967) suggested, but simply consists of logical rather than empirical statements.

INDUCTIVE AND DEDUCTIVE CLASSIFICATION

Summarizing the inductive taxonomic approach, we might say that it is convergent: based on one set of data (a), criteria (b) and aims (c), only one optimal system can be constructed. Opposite to this is the deductive approach. Since classification is dependent on our own (a), (b) and (c) only, one is free to choose any system one likes, as long as the underlying reasoning is consistent, i.e., as long as the classification does not conflict with the pre-established criteria. One can pose a particular system as a taxonomic hypothesis; the consistency of the reasoning can then be verified experimentally by deduction. Using the same set of data, criteria and aims, widely different hypotheses can be compared, and we might therefore say that this approach is divergent. Altering (b) and (c), the same hypothesis can be evaluated differently. Similar testing of systems by means of random samples of characters has already been attempted by Gower (1974), Correll (1977) and Barnett et al. (1975).

A TAXONOMIC EXPERIMENT

In the experiment below, two modern systems of Ascomycetes [Figs. 14.1 (I) and 14.2 (II)], for the construction of which I am indebted to Drs. J.A. von Arx (I) and D. Malloch (II), will be considered. The constituents of both systems are strictly comparable. The units have been chosen in such a way that they could be connected in a meaningful order, whereas within the

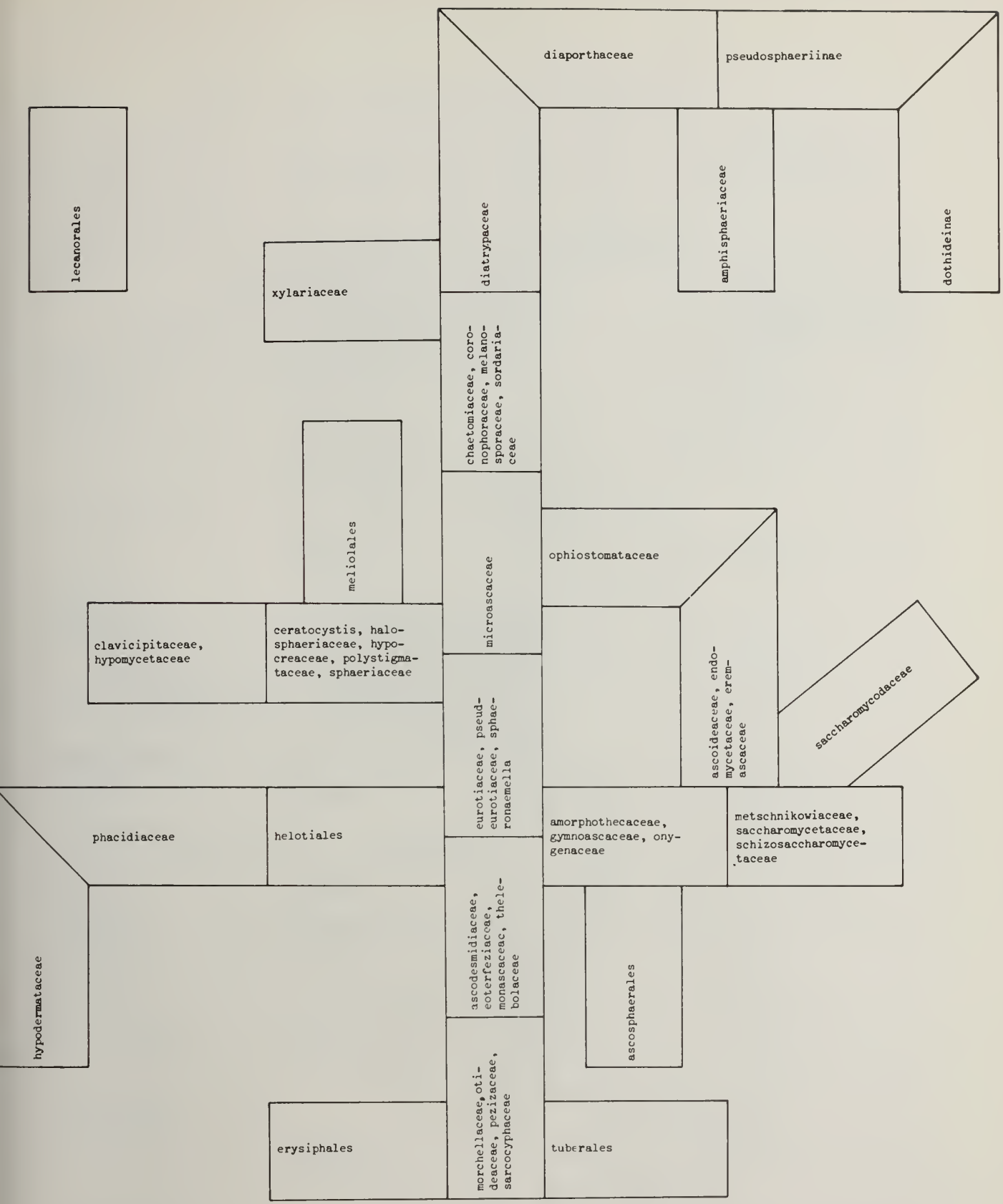


Fig. 14.1 System-I of the Ascomycetes.

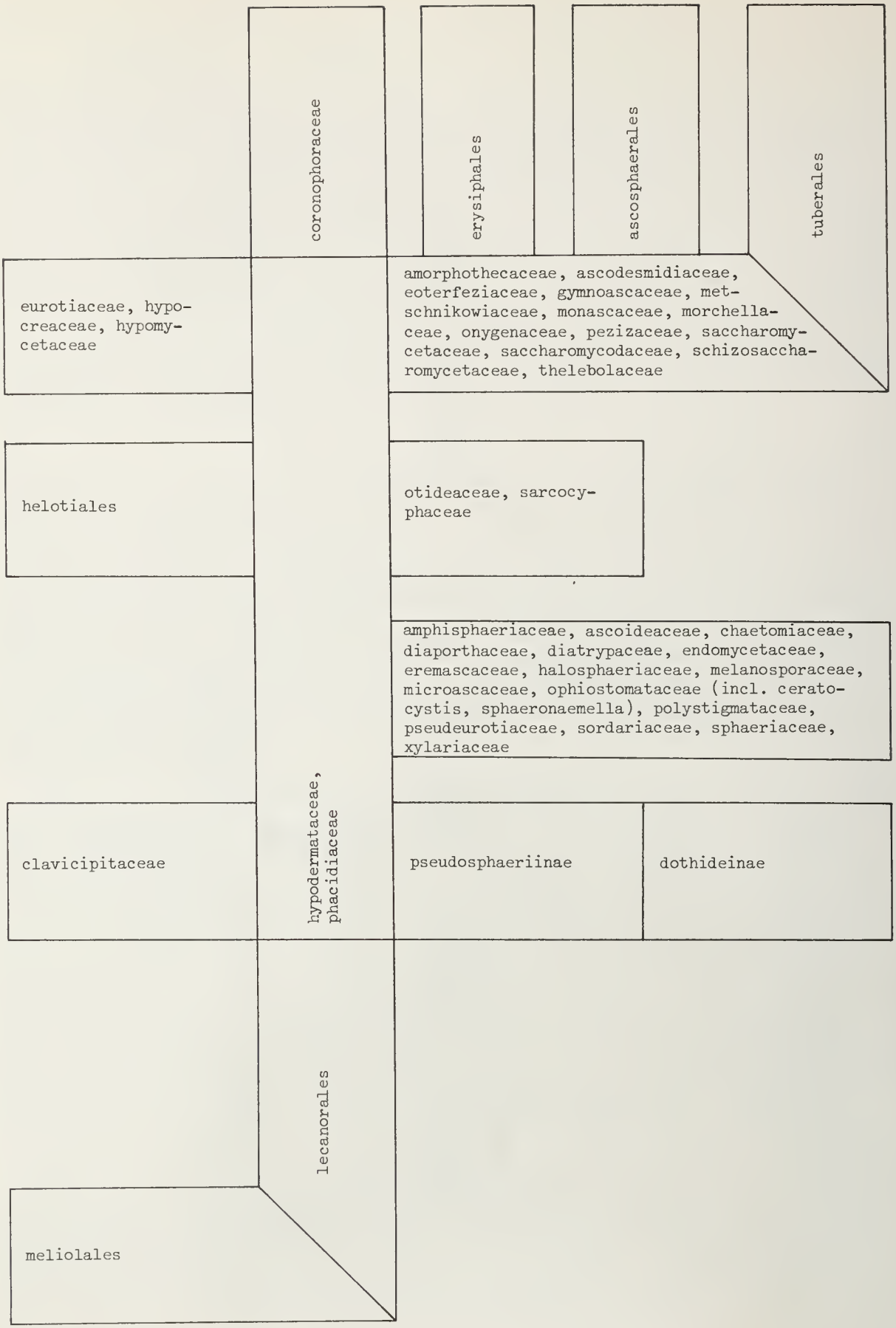


Fig. 14.2 System-II of the Ascomycetes.

Table 14.1. The screened genera of Ascomycetes with their anamorphs.

1. Amorphothecaceae:	
Amorphotheca	- *Hormoconis*
2. Amphisphaeriaceae:	
Amphisphaeria	- *Dendryphiopsis*
Apiospora	- *Arthrinium* *Nigrospora* *Pteroconium*
Blogiascospora	- *Seiridium*
Broomella	- *Pestalotia*
Ceriospora	- *Chaetoconis*
Discostroma	- *Seimatosporium*
Griphosphaeria	- *Fusarium* *Seimatosporium*
Griphosphaerioma	- *Labridella*
Lepteutypa	- *Hyalotiella* *Seiridium*
Pestalosphaeria	- *Pestalotia*
Physalospora	- *Arthrinium*
Pseudomassaria	- *Beltraniella*
3. Ascodesmidiaceae:	
Eleutherascus	- *Nodulisporium*-like
4. Ascosphaerales:	
Ascosphaera	- *Chrysosporium*
5. Ascoideaceae:	
Ambrosiozyma	- *Raffaelea*-like
Ascoidea	- unnamed
Botryoascus	- *Raffaelea*-like
Cephaloascus	- *Hyalodendron*-like
Hormoascus	- unnamed
Hyphopichia	- *Sporothrix*-like
Saccharomycopsis	- unnamed
Stephanoascus	- *Sporothrix*-like
6. Ceratocystis:	
Ceratocystis	- *Chalara* *Chalaropsis* *Thielaviopsis*
7. Chaetomiaceae:	
Chaetomium	- *Botryotrichum* *Humicola*
Corynascus	- *Sepedonium*-like
Farrowia	- *Botryotrichum*
Thielavia	- *Myceliophthora*-like
Zopfiella	- *Humicola*
8. Clavicipitaceae:	
Byssostilbe	- *Tilachlidium*
Claviceps	- *Sphacelia*
Cordyceps	- *Akanthomyces* *Gibellula* *Hirsutella* *Hymenostilbe* *Verticillium*
Epichloë	- *Sphacelia*
Ophiocordyceps	- *Hirsutella*
9. Coronophoraceae:	
Thaxteria	- *Oedemium*
10. Diaporthaceae:	
Apiognomonia	- *Discula*
Ceratosphaeria	- *Pyricularia*
Cryptodiaporthe	- *Chondroplea* *Discella*
Diaporthe	- *Phomopsis*
Endothia	- *Endothiella*
Gaeumannomyces	- *Phialophora*
Gnomonia	- *Cylindrosporella* *Discula* *Monostichella* *Zythia*
Gnomoniella	- *Cylindrosporella*
Hercospora	- *Rabenhorstia*
Melanamphora	- unnamed
Melanconis	- *Melanconium*
Melanochaete	- *Sporoschisma*
Melogramma	- *Cytosporina*
Prosthecium	- *Stilbospora*
Pseudovalsa	- *Coryneum*
Valsa	- *Cytospora*
Valseutypella	- *Cytospora*
11. Diatrypaceae:	
Diatrype	- *Libertella*
Diatrypella	- *Libertella*
Eutypa	- *Cytosporina* *Phomopsis*

Eutypella	- *Cytosporina* *Phomopsis*
Quaternaria	- *Libertella*

12. Dothideinae:

Acanthotheciella	- *Ypsilonia*
Alina	- *Septoidium*
Asterina	- *Asterostomella*
Asterodothis	- *Asterostromina*
Atichia	- *Actinomma*
Aulographina	- *Bahusakala*
Bagnisiella	- *Haplosporella*
Batistinula	- *Triposporium*
Botryosphaeria	- *Botryodiplodia* *Dothiorella* *Haplosporella* *Lasiodiplodia* *Leptodothiorella*
Clypeolella	- *Clasterosporium* *Mitteriella* *Sarcinella*
Dothiora	- *Dothichiza* *Hormonema*
Elsinoë	- *Melanobasidium* *Sphaceloma*
Eupelte	- *Clasterosporium* *Pirozynskia* *Septoidium* *Sporidesmium*-like
Eutryblidiella	- *Diplodia*-like *Phoma*-like
Farlowiella	- *Acrogenospora*
Guignardia	- *Colletotrichella* *Hormonema* *Leptodothiorella* *Phyllosticta* *Placosphaeria* *Selenophoma*
Hysterium	- *Coniosporium* *Hysteropycnis*
Hysterographium	- *Hysteropycnis*
Leptoguignardia	- *Dothichiza*
Leptopeltopsis	- *Leptothyrium*
Melioliphila	- *Chionomyces* *Eriomycopsis*
Mytilidion	- *Septonema*
Neoparodia	- *Chuppia* *Sarcinella*
Ophioparodia	- *Septoidium*
Parodiella	- *Septoidium*
Parodiellina	- *Septoidium*
Perisporiopsis	- *Septoidium*
Pilgeriella	- *Septoidium*
Prillieuxina	- *Leprieurina*
Pringsheimia	- *Dothichiza* *Hormonema*
Pycnothyrium	- *Leptothyrium*
Schiffnerula	- *Mitteriella* *Sarcinella*
Sydowia	- *Dothichiza* *Hormonema*
Trabutia	- *Baeumleria*
Uleothyrium	- *Septothyrella*
Xenomeris	- *Hormonema*
Yamamotoa	- *Clasterosporium* *Mitteriella* *Sarcinella*

13. Endomycetaceae:

Dipodascus	- *Geotrichum*
Endomyces	- *Geotrichum*

14. Eoterfeziaceae:

Cleistothelebolus	- unnamed

15. Eremascaceae:

Eremascus	- unnamed

16. Erysiphales:

Erysiphe	- *Oidium*
Leveillula	- *Oidiopsis*
Microsphaera	- *Oidium*
Phyllactinia	- *Ovulariopsis*
Podosphaera	- *Oidium*
Sphaerotheca	- *Oidium*
Uncinula	- *Oidium*

17. Eurotiaceae:

Aphanoascus	- *Paecilomyces*
Byssochlamys	- *Paecilomyces*
Cephalotheca	- *Paecilomyces*
Chaetosartorya	- *Aspergillus*
Dichlaena	- *Aspergillus*
Dichotomomyces	- *Polypaecilum*
Emericella	- *Aspergillus*
Ephemeroascus	- *Verticillium*
Eupenicillium	- *Penicillium*

Eurotium - *Aspergillus*
Fennellia - *Aspergillus*
Hamigera - *Penicillium*
Hemicarpenteles - *Aspergillus*
Hemisartorya - *Aspergillus*
Neosartorya - *Aspergillus*
Penicilliopsis - *Penicillium*
Sagenoma - *Acremonium*
Syncleistostroma - *Aspergillus*
Talaromyces - *Paecilomyces*
Penicillium
Thermoascus - *Paecilomyces*
Polypaecilum
Trichocoma - *Penicillium*
Warcupiella - *Aspergillus*

18. Gymnoascaceae:

Ajellomyces - *Blastomyces*
Anixiopsis - *Chrysosporium*
Apinisia - *Chrysosporium*
Arachnotheca - *Geotrichum*
Arthroderma - *Chrysosporium*
Keratinomyces
Trichophyton
Auxarthron - *Malbranchea*
Byssoascus - *Oidiodendron*
Emmonsiella - *Histoplasma*
Gymnoascus - *Chrysosporium*
Keratinophyton - *Chrysosporium*
Myxotrichum - *Malbranchea*
Oidiodendron
Nannizzia - *Microsporum*
Pseudogymnoascus - *Chrysosporium*

19. Halosphaeriaceae:

Corollospora - *Clavariopsis*
Halosphaeria - *Periconia*
Remispora - *Periconia*

20. Helotiales:

Ascocalyx - *Bothrodiscus*
Brunchorstia
Ascocorticium - *Acrodontium*
Ascocoryne - *Coryne*
Phialophora
Atropellis - *Fuckelia*
Bisporella - *Cystodendron*
Blumeriella - *Phloeosporella*
Botryotinia - *Amphobotrys*
Botrytis
Calloria - *Cylindrocolla*
Calloriopsis - *Eriomycopsis*
Calycellina - *Chaetochalara*
Ciboria - *Myrioconium*
Crumenulopsis - *Digitosporium*
Dermea - *Micropera*
Diplocarpon - *Actinonema*
Entomosporium
Marssonina
Discohainesia - *Hainesia*
Pilidium
Drepanopeziza - *Gloeosporidiella*
Marssonina
Godronia - *Fuckelia*
Topospora
Habrocystis - *Cryptosporiopsis*
Heterosphaeria - *Heteropatella*
Holwaya - *Crinula*
Hyaloscypha - *Chaetochalara*
Clathrosphaeria
Haplographium
Hymenoscyphus - *Idriella*
Varicosporium
Leptotrochila - *Sporonema*
Mollisia - *Anguillospora*
Phialophora
Monilinia - *Monilia*
Ocellaria - *Cryptosporiopsis*
Ovulinia - *Ovulitis*
Pestalopezia - *Pestalotia*
Pezicula - *Cryptosporiopsis*
Phlyctaena
Phaeosclerotinia - *Monilia*
Pragmopora - *Pragmopycnis*
Pycnopeziza - *Acarosporium*
Pyrenopeziza - *Phialophora*
Rhabdocline - *Rhabdogloeum*
Rutstroemia - *Myrioconium*
Sageria - *Ascoconidium*
Sclerotinia - *Myrioconium*
Seaverinia - *Verrucobotrys*
Septotinia - *Septotis*
Streptotinia - *Streptobotrys*
Trochila - *Cryptocline*

Tympanis - *Sirodothis*

Xylogramma - *Cystotricha*

21. Hypocreaceae:

Calonectria - *Acremonium*
Cylindrocladium
Fusarium
Verticillium

Gibberella - *Fusarium*

Hypocrea - *Gliocladium*
Trichoderma

Melanopsamma - *Stachybotrys*

Nectria - *Acremonium*
Cylindrocarpon
Fusarium
Gliocladium
Heliscus
Kutilakesopsis
Myrothecium
Stilbella
Tuberculariа
Tuberculispora
Verticillium
Zythia

Neocosmospora - *Acremonium*

Ophionectria - *Antipodium*

Podostroma - *Trichoderma*

Pseudonectria - *Sesquicillium*
Volutella

Roumegueriella - *Phialocephala*

Scoleconectria - *Zythiostroma*

Thyronectria -- *Tubercularia*
Zythiostroma

22. Hypodermataceae:

Darkera - *Tiarosporella*

Duplicaria - *Melasmia*

Lirula - *Hypodermina*

Lophodermium - *Labrella*
Leptostroma

Micraspis - *Peripéridium*

Ploioderma - *Leptostroma*

Potebniamyces - *Hormonema*
Phacidiopycnis

Rhytisma - *Melasmia*

23. Hypomycetaceae:

Hypomyces - *Cladobotryum*
Mycogone
Sepedonium
Sibirina
Trichothecium
Verticillium

Peckiella - *AcremoniumFennellia*
Sepedonium

Pyxidiophora - *Chalara*-like

24. Lecanorales:

25. Melanosporaceae:

Melanospora - *Acremoniella*

26. Meliolales:

27. Metschnikowiaceae:

Ashbya - unnamed

Metschnikowia - unnamed

Nematospora - unnamed

28. Microascaceae:

Kernia - *Graphium*
Scopulariopsis

Leuconeurospora - *Chrysosporium*-like

Microascus - *Scopulariopsis*
Wardomyces

Petriella - *Graphium*
Scopulariopsis

Petriellidium - *Graphium*
Scedosporium

29. Monascaceae:

Monascus - *Basipetospora*

Xeromyces - *Fraseriella*

30. Morchellaceae:

Morchella - *Costantinella*

31. Onygenaceae:

Leucothecium - unnamed

Onygena - unnamed

Xynophilum - unnamed

32. Ophiostomataceae:

Ceratocystiopsis - *Sporothrix*

Ophiostoma - *Graphium*
Graphilbum
Hyalopesotum
Hyalorhinocladiella
Leptographium
Pachnodium
Pesotum
Phialographium
Raffaelea
Sporothrix
Verticicladiella

33. Otideaceae:

Geopyxis - *Nodulisporium*-like

Korfiella - *Conoplea*

34. Pezizaceae:

Iodophanus - *Oedocephalum*

Peziza - *Chromelosporium*
Oedocephalum
Ostracoderma

Pyronema - *Oedocephalum*

Sphaerosporella - *Dichobotrys*

Trichophaea - *Dichobotrys*

35. Phacidiaceae:

Phacidium - *Ceuthospora* auctt.
Neottiospora

36. Polystigmataceae:

Glomerella - *Colletotrichum*

37. Pseudeurotiaceae:

Cryptendoxyla - *Chalara*

Emericellopsis - *Acremonium*

Fragosphaeria - *Sporothrix*-like

Hapsidospora - *Acremonium*

Mycoarachis - *Acremonium*

Nigrosabulum - *Acremonium*

Pseudeurotium - *Acremonium*
Sporothrix-like

38. Pseudosphaeriinae:

Aithaloderma - *Cicinnobella*
Leptoxyphium
Microxyphium auctt.

Asteromassaria - *Scolecosporium*

Brooksia - *Hiospira*

Caryospora - *Asterostomella*

Clathrospora - *Alternaria*

Cochliobolus - *Curvularia*
Drechslera

Comoclathris - *Alternaria*

Cicurbitaria - *Camarosporium*
Diplodia
Phoma
Pleurostromella

Curreya - *Coniothyrium*

Dictyotrichiella - *Exophiala*

Didymella - *Ascochyta*
Phoma

Didymosphaeria - *Dendrophoma*
Periconia

Dimerina - *Ectosticta*

Dimerium - *Cicinnobella*
Ectosticta

Euantennaria - *Antennatula*
Hormisciomyces

Eudarluca - *Darluca*

Gemmamyces - *Megaloseptoria*

Gibberidea - *Pleurostromella*

Gilletiella - *Ascochyta*

Gillotia - *Asteromella*

Glyphium - *Peyronelia*

Herpotrichia - *Pyrenochaeta*

Keissleriella - *Ascochyta*
Denemasporium

Leptosphaeria - *Alternaria*
Camarosporium
Hendersonia
Phoma
Rhabdospora
Stagonospora

Limacinia - *Capnocybe*
Capnophialophora
Hormiokrypsis

Limacinula - *Shanoria*

Magnaporthe - *Nakataea*

Massarina - *Ceratophoma*
Coniothyrium
Phoma
Pyricularia

Melanomma - *Aposphaeria*
Pseudospiropes

Meliolina - *Catenularia*-like

Metacapnodium - *Capnobotrys*
Capnophialophora

Microcyclus - *Asteromella*
Cercospora
Passalora
Pazschkeella

Mycosphaerella - *Asteromella*
Cercoseptoria
Cercospora
Cercosporella
Cladosporium
Fusicladiella
Heterosporium
Miuraea
Ovularia
Passalora
Phloeospora
Polythrincium
Ramularia
Septoria
Stigmina

Ophiocapnocoma - *Capnocybe*
Capnophialophora
Hormiokrypsis

Otthia - *Diplodia*
Stigmina

Paraphaeosphaeria - *Coniothyrium*
Hendersonia

Phaeosphaeria - *Hendersonia*

Pleomassaria - *Prosthemium*

Pleospora - *Alternaria*
Dendryphion
Phoma
Stemphylium

Podonectria - *Tetranacrium*

Preussia - *Phoma*

Protocucurbitaria - *Phoma*

Pyrenophora - *Drechslera*

Setosphaeria - *Exserohilum*

Sphaerulina - *Cercospora*
Septoria

Splanchnonema - *Prosthemium*
Steganosporium

Strigopodia - *Capnophialophora*
Hormisciella

Thaxteriella - *Helicoma*

Trematosphaeria - *Phoma*

Trichopeltheca - *Plokamidomyces*
Trichothallus

Trichothyrium - *Isthmospora*

Triposporiopsis - *Triposporium*

Tubeufia - *Helicosporium*

Venturia - *Cladosporium*
Fusicladium
Pollaccia
Spilocaea

Westerdykella - *Phoma*

39. Saccharomycetaceae:

Citeromyces - unnamed

Cyniclomyces - unnamed

Dekkera - *Brettanomyces*

Hansenula - unnamed

Issatchenkia - unnamed

Kluyveromyces - unnamed

Lipomyces - unnamed

Lodderomyces - unnamed

Pachysolen - unnamed

Pichia - unnamed

Saccharomyces - unnamed

Schwanniomyces - unnamed

Torulaspora - unnamed

Wickerhamiella - unnamed

Williopsis - unnamed

Wingea - unnamed

Zygosaccharomyces - unnamed

40. Saccharomycodaceae:

Hanseniaspora - *Kloeckera*

Nadsonia - unnamed

Saccharomycodes - unnamed

Wickerhamia - unnamed

41. Sarcoscyphaceae:

Desmazierella - *Verticicladium*

Plectania - *Conoplea*

Urnula - *Conoplea*
Strumella

42. Schizosaccharomycetaceae:

Schizosaccharomyces - unnamed

43. Sordariaceae:

Apiosordaria - *Cladorrhinum*

Cercophora - *Phialophora*

Coniochaeta - *Phialophora*

Helminthosphaeria - *Diplococcium*

Lasiosphaeria - *Helicoma*

Neurospora - *Monilia*

Parkerella - *Cyphellophora*-like

44. Sphaeriaceae:

Chaetosphaeria - *Catenularia*
Chloridium
Codinaea
Gonytrichum
Menispora
Sporoschisma
Stachybotrys
Zanclospora

Niesslia - *Monocillium*

Plectosphaerella - *Fusarium*

45. Sphaeronaemella:

Sphaeronaemella - *Gabarnaudia*

46. Thelebolaceae:

Thecotheus - *Acrodontium*-like

Thelebolus - unnamed

47. Tuberales:

48. Xylariaceae:

Ascotricha	- *Dicyma*
Graphostroma	- *Nodulisporium*
Hypoxylon	- *Basidiobotrys* *Geniculosporium* *Nodulisporium* *Periconiella*
Nummularia	- *Basidiobotrys*
Poronia	- *Basidiobotrys*
Rosellinia	- *Dematophora* *Nodulisporium*
Xylaria	- *Nodulisporium* *Padixonia*

Table 14.2 List of characters used.

1. parasitic on phanerogams / not parasitic on phanerogams
2. osmophilic / not osmophilic
3. coprophilous / not coprophilous
4. parasitic on man or animals / not parasitic on man or animals
5. ambrosia fungi / not ambrosia fungi
6. hyperparasitic / not hyperparasitic
7. budding cells present / absent
8. mycelium torulose / not torulose
9. stromata present / absent
10. setae or peridial appendages present / absent
11. terricolous / not terricolous
12. perithecial or pseudothecial ascomata present / absent
13. pycnidial conidiomata present / absent
14. fruit bodies pale / dark
15. fruit bodies more or less globose / not globose
16. fruit bodies volcano-shaped / not volcano-shaped
17. cavities developing by dissolution of stromal cells / not lysigenous
18. cavities regular / irregular or multilocular
19. fruit bodies with preformed ostiole / without preformed ostiole
20. fruit bodies opening by deliquescence / not opening by deliquescence
21. fruit bodies splitting open / not splitting open
22. fruit bodies beaked / not beaked
23. periphyses present / absent
24. fruit bodies cellular / composed of interwoven hyphae
25. cylindrical cells present on walls of fruit bodies / absent
26. walls of fruit bodies pseudoparenchymatous / not pseudoparenchymatous
27. walls of fruit bodies of textura epidermoidea / not of textura epidermoidea
28. paraphyses or pseudoparaphyses present / absent
29. apothecial ascomata present / absent
30. acervular conidiomata present / absent
31. fruit bodies stalked / sessile or immersed
32. hymenium flat or concave / not flat or concave
33. hymenium of irregular shape / not of irregular shape
34. fruit bodies with epithecium / without epithecium
35. asci unitunicate / bitunicate
36. asci operculate / inoperculate
37. asci with apical apparatus / without apical apparatus
38. asci amyloid / not amyloid
39. asci extending above the hymenium / not extending above the hymenium
40. asci globose to broadly ellipsoidal / more or less cylindrical
41. asci catenulate / not catenulate

42. asci containing 1-6 ascospores / more than 7 ascospores
43. asci evanescent / persistent
44. ascospores without mucous sheath / with mucous sheath
45. ascospores with appendages / without appendages
46. ascospores with germ pores or germ slits / without germ pores or germ slits
47. ascospores hyaline / pigmented
48. ascospores smooth / ornamented
49. ascospores one-celled / septate
50. ascospores globose to ellipsoidal / not globose to ellipsoidal
51. ascospores fusiform to thread-like / not fusiform to thread-like
52. ascospores straight / curved
53. ascospores breaking up into separate cells / not breaking up
54. conidiophores single / aggregated
55. conidiophores differentiated / scarcely or not differentiated
56. conidiophores branched verticillately, penicillately or dichotomously / unbranched or irregularly branched
57. conidiophores basauxic / acroauxic
58. conidiogenous cells differentiated / integrated
59. conidiogenous cells often intercalary / not intercalary
60. conidiogenous cells ventricose / not ventricose
61. arthric conidia present / absent
62. blastic conidia present on hyphae / absent from hyphae
63. thallic conidia present / absent
64. conidiogenous cells monoblastic / polyblastic
65. fertile rachides differentiated / integrated
66. fertile parts of conidiogenous cells elongate / short
67. blastic conidia single or in basipetal chains / in acropetal chains
68. conidia formed percurrently / not formed percurrently
69. collarette present / absent
70. endogenous conidia formed by cleavage / formed by blastic growth
71. conidia dry / slimy
72. conidia synchronous / not synchronous
73. conidia hyaline / pigmented
74. conidia smooth / verrucose
75. conidia straight / curved
76. conidia furcate / not furcate
77. conidia coiled / not coiled
78. conidia with appendages / without appendages
79. conidia one-celled / septate

units no order could be found (Table 14.1).

The list of characters on which the random tests will be based was compiled as follows. Out of every five higher taxa, combined or connected in the most dispersive of systems-I and -II, an Ascomycete genus with its first listed anamorph (Table 14.1) was selected at random. All qualitative characters known in these genera or form-genera were abstracted from the literature; in this way a more or less representative group of characters, used at (form-) generic level, was obtained. Most quantitative characters had to be neglected, since their comparison is far too laborious; many specific qualitative characters were neglected too, since they proved to be hardly comparable over higher taxa. This does not affect the principle of system-testing, since only a random sample of characters is needed. In addition to the list of characters used at the micro-level, all key-features of higher taxa were compiled from the keys to larger Ascomycete groups given by von Arx (1967), in order to find the more general properties which are often unstated in the descriptions at lower levels. The list was supplemented with characters from similarly screened keys to imperfect genera (Barnett & Hunter 1972). The list thus drafted comprises 79 characters (Table 14.2).

For every genus the presence or absence of each character(-state) was scored. In case of doubt, or if both character-states occurred, presence as well as absence was filled out; in case of noncomparability the character was neglected. A severe problem in comparing single characters over higher taxa is the application of several terms in the literature which are correlated to the limits of taxa; consequently they are necessarily supportive to the system. For example, the ascoma of a member of the Pseudosphaeriinae is referred to as a pseudothecium, regardless of the fact that its structure may be very similar to the ascomata of some fungi having apothecia. Note that this may prohibit an objective analysis of the system.

The systems to be compared are principally based on the properties of the teleomorphs. In order to include as many secondary characters (viz., characters on which the system has not explicitly been based) as possible, only those taxa are included in which at least one anamorph is known.

In addition to both systems mentioned above, a control system was constructed by making small cards of each unit, mixing them up and having them connected according to certain rules by someone to whom the cards were meaningless.

THE MEASURE OF CONSISTENCY

In the tests, the classification criteria 1a, 1b, 1c and 2, as outlined below, are applied.

1. EMPIRICAL DATA

a. HOMOGENEITY

Concerning the distribution of character-states, it is assumed that the borders of taxa should coincide with the limits of character-states. In other words: a character-state ending in the middle of a taxon (viz., 50% matching) is minimally supportive to that part of the system. Consequently if the number of genera of taxon S with character-state i (S_i) is 50%, that is equal to half the possible number of matches in that taxon (S_t), is the minimal score; then $S_i - \frac{1}{2}S_t = 0$. The maximum score, normalized to 1, is $(S_i - \frac{1}{2}S_t) / \frac{1}{2}S_t = 1$. Summing this up and normalizing this over all taxa (n) and all characters (p), we arrive at the following formula:

HOMOGENEITY:

$$\frac{1}{np} \sum^{np} \frac{S_i - \frac{1}{2}S_t}{\frac{1}{2}S_t} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (1)$$

in which:

n = number of taxa,

p = number of characters,

S_i = number of genera of taxon S with character-state i,

S_t = number of genera in taxon S.

Formula (1) was initially applied to a control-taxon composed of groups which were treated both in system-I and -II as unrelated (Diatrypaceae, Erysiphales, Metschnikowiaceae, Pseudeurotiaceae and Sphaeriaceae). The result was 0.77. Consequently any taxon with a homogeneity near or below 0.77 is regarded as unacceptably heterogeneous. Taxa with homogeneity = 1.00, on the other hand, are maximally homogeneous. There are no criteria to establish the minimum level of acceptability.

The average homogeneities of systems I and II are about equally high: 0.87 and 0.86 respectively. There are, however, large differences between the taxa. In system-I five taxa (= 22%), and in system-II four taxa (= 33%), are below 0.80, consequently being unacceptably heterogeneous. If we choose 0.85 as a minimum acceptable level of homogeneity these figures rise to 43 and 42% respectively. If we assume that a score of 0.90 is rather good, we find that 39% of system-I and 33% of system-II is acceptable. Thus, system-I is slightly better in this respect that system-II. The difference might be explained by the taxa being rather small in system-I: the scores in the control-system, most taxa of which were accidentally composed of only one or a few groups, were also very high.

b. CORRELATION OF KEY-FEATURES

Heterogeneous taxa may well reflect the tendencies present in the data, as has already been explained in the discussion of polythetic groups. The taxa should then be recognizable by their mutual discontinuities. The criterion for separation is that the bordering genera of two taxa are more dissimilar than the average dissimilarities within the taxa. This can only be measured if the genera within the taxa are ordered, because, if not, the bordering genera are not known. In the system under consideration there is no such order and hence there is no objective basis for the establishment of taxonomic borders. The establishment of 'polythetic, unordered groups' is, therefore, rejected for use in taxonomy. The only criterion left for the evaluation of discontinuities is still the correlation of key-features: if a taxon differs by a large number of characters from its neighbouring taxon, then the borderline between these taxa is well chosen. Therefore, we take the number of character-states ending at the border of a taxon (p_L) as a percentage of the total number of comparable characters (p). Summing this up and normalizing this over the number of bordering taxa (n_L), we arrive at the following expression:

CORRELATION:

$$\frac{1}{n_L} \sum^{n_L} \frac{p_L}{p} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (2)$$

in which:

n_L = number of bordering taxa,

p_L = number of character-states of taxon S ending at the border of that taxon,

p = number of characters.

If a taxon is heterogeneous, most of the possible character-states occur to a greater or lesser extent. This means that there are only very few characters left for an eventual black-white distinction from other taxa. If, for example, we compare the unrelated but heterogeneous Helotiales and Dothideinae, none of the 79 characters used is diagnostic. The homogeneous Coronophoraceae and Phacidiales, on the other hand, are separated by 18 key-features. Therefore this coefficient should be considered in relation to the homogeneity of the compared taxa.

In addition, the key-feature is a relative concept, being dependent on the compared taxa: if these are unrelated, the number of key-features is large, but if they are similar, only a few key-features are available. In conclusion, a high correlation coefficient is an indication that the borderline is well chosen, but also that the bordering taxa are unrelated, particularly when the taxa are heterogeneous. A low coefficient, particularly between homogeneous taxa, means that the taxa are close and that the borderline may be arbitrarily chosen.

The fact that conclusions from the correlation of key-features are rather ambiguous, prohibits a general comparison of both systems. the differences are, however, very conspicuous (in Figs. 14.3 and 14.4 the results have been taken as a percentage of the maximum score). In system-I the coefficients are remarkably low, with only a few exceptions. The Erysiphales and Helotiales may be wrongly connected, having high coefficients, and similarly the connection between Sphaeriaceae etc., and Eurotiaceae etc., is open to discussion. The coefficient is also rather high in the yeast-like and related fungi, but here the groups are rather homogeneous. In system-II, on the other hand, most of the numbers are very high, often amply exceeding those found in the control-system. Consequently the question arises whether the taxa in system-II are correctly connected.

c. SEQUENCE OF TAXA

If a character occurs scattered through the system, it is not particularly supportive to that system. The number of discontinuities in the distribution of each character should therefore be as low as possible. The correctness of the sequence of the taxa can consequently be measured by counting those numbers of discontinuities. The minimum is zero, the maximum $\frac{1}{2}n - \frac{1}{2}$ (nominal; see Fig. 14.5). The maximum of this notation is normalized to 1 and then summed over the number of characters, to give the following expression:

SEQUENCE:

$$\frac{1}{p} \sum^{p} \frac{[\frac{1}{2}n - \frac{1}{2}]^{\text{nom.}} - M}{[\frac{1}{2}n - \frac{1}{2}]^{\text{nom.}}} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (3)$$

in which:

p = number of characters,

n = number of taxa,

M = number of discontinuities.

Before the results are given, a related topic will be discussed.

2. *PHYLOGENETIC THEORY*

A character with a distribution contradictory to the majority of the characters is supposed to point to common ancestry or parallel evolution of dissimilar groups (Farris 1966). The relative distance between unconnected taxa in which the character is found is a measure for this phylogenetic significance. The maximum distance is $n_{d(max)}$ taxa; the minimum is zero. The distance is taken as a percentage of the maximal possible distance $[n_{d(tot)}]$ in the system concerned, both factors being dependent on the branching pattern of that system. The value of the character decreases if it is also scattered in other taxa; scattering being expressed by the number of discontinuities (M). Summing up over p characters and normalizing gives the following expression:

PHYLOGENY:

$$\frac{1}{p} \sum^{p} \frac{n_{d(max)}}{M.n_{d(tot)}} \quad \ldots\ldots\ldots\ldots\ldots\ldots\ldots \quad (4)$$

in which:

p = number of characters,

$n_{d(max)}$ = number of taxa lying between two maximally remote taxa with character-state i,

$n_{d(tot)}$ = number of taxa lying between two maximally remote taxa,

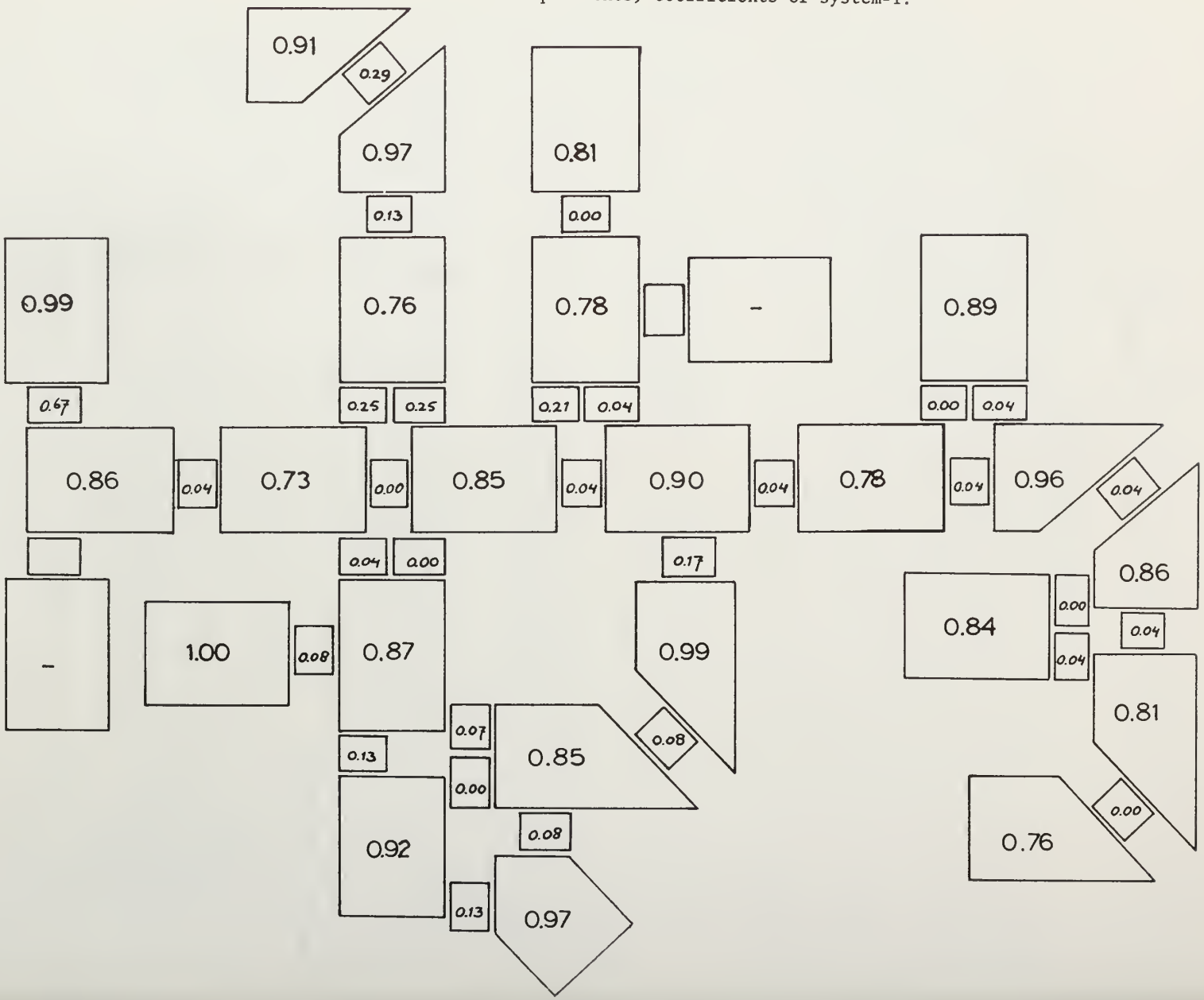
M = number of discontinuities.

In general, all distances should be minimized, since similar groups without contradictory characters are supposedly monophyletic, which is the simplest possible systematization. If there are conspicuously contradictory characters, one can either decide to neglect these by classifying mainly on average similarity, aiming at optimally homogeneous groups, or to use these as principal guide-lines for classification, accepting some heterogeneity in the groups.

Applying coefficients (3) and (4) to systems-I and -II, we find that the systems have different accents. In system-I the groups are established on the basis of optimal similarity. Only a few characters are restricted to a part of the system, the sequence-coefficient rarely being 1 (Fig. 14.7), and in a number of cases a potential regrouping is accepted in the form of characters with a high phylogenetic value (e.g., 7, 8, 21, 29, 69, 75; Fig. 14.7). Note that the characters of ascospores and of the anamorphs hardly play any role in this system.

The shape of system-II is well suited to expressing phylogenetic suppositions. The group Hypodermataceae/Phacidiaceae has been taken as a basis from which other taxa can be thought to be derived. A character present in this group -- even if only in part of the group -- is very likely to lack discontinuities (Fig. 14.5). However, a character with the

Fig. 14.3 Results of homogeneity (large compartments) and correlation (small compartments) coefficients of system-I.



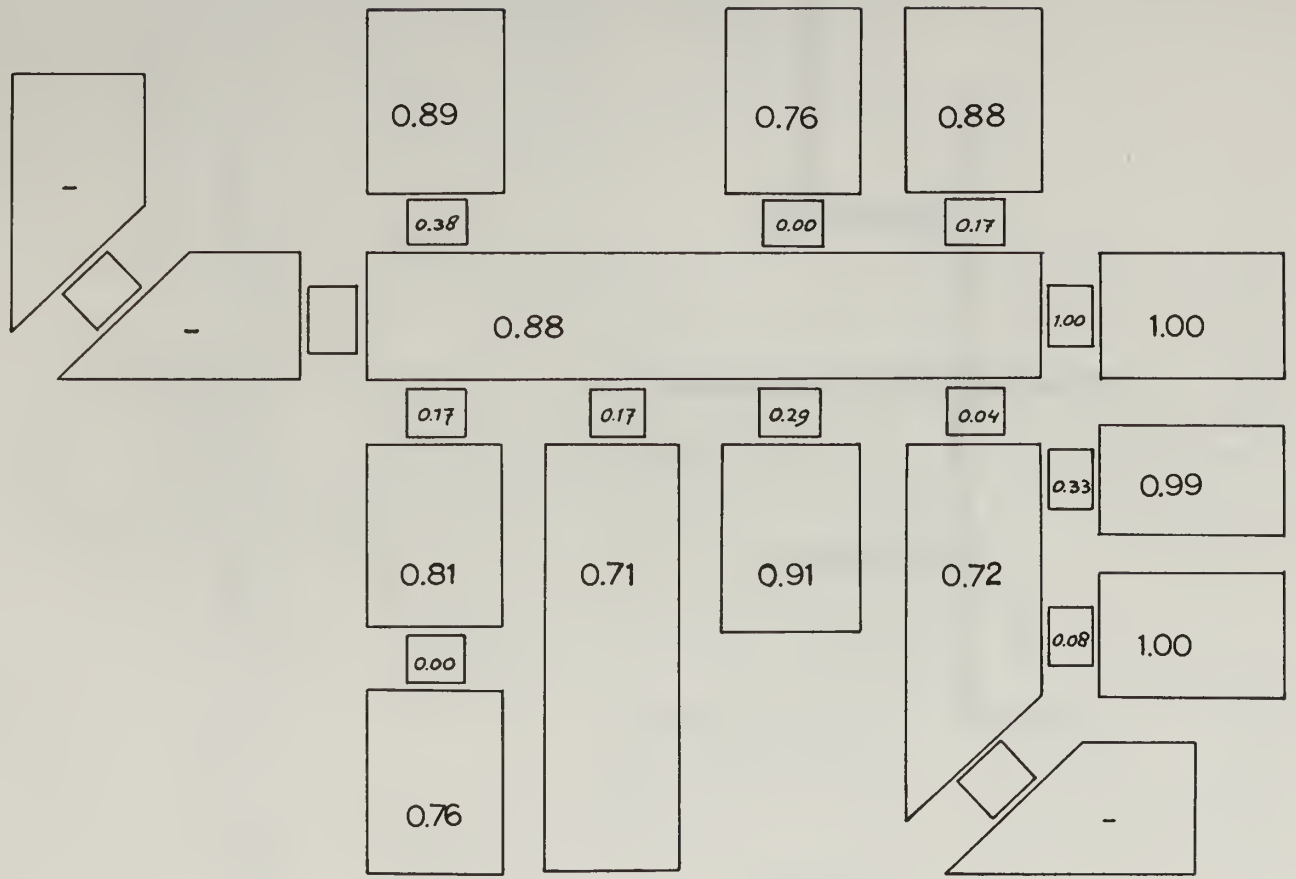


Fig. 14.4 Results of homogeneity (large compartments) and correlation (small compartments) coefficients of system-II.

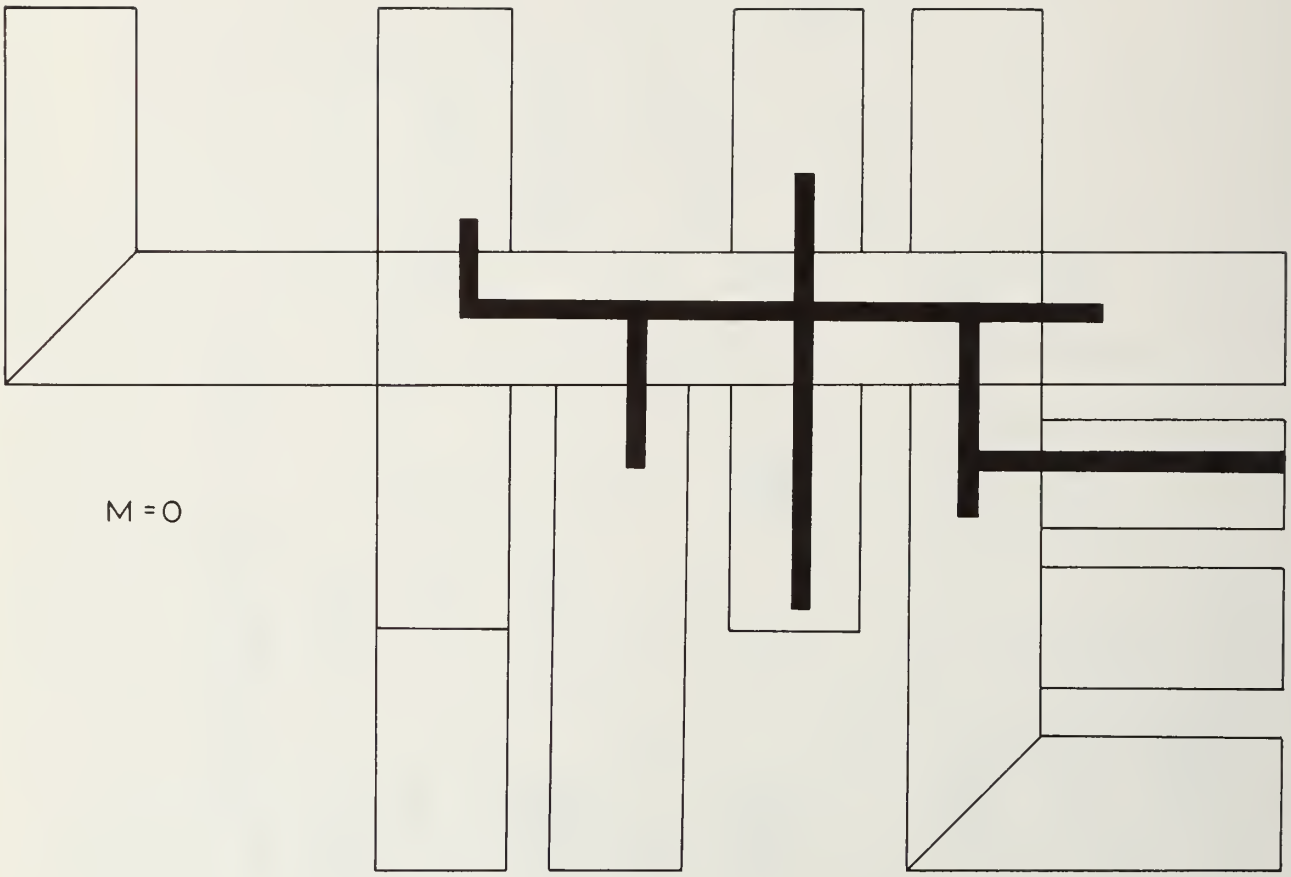


Fig. 14.5 Diagrammatic representation of coherent distribution of a certain character-state in system-II. M = number of discontinuities.

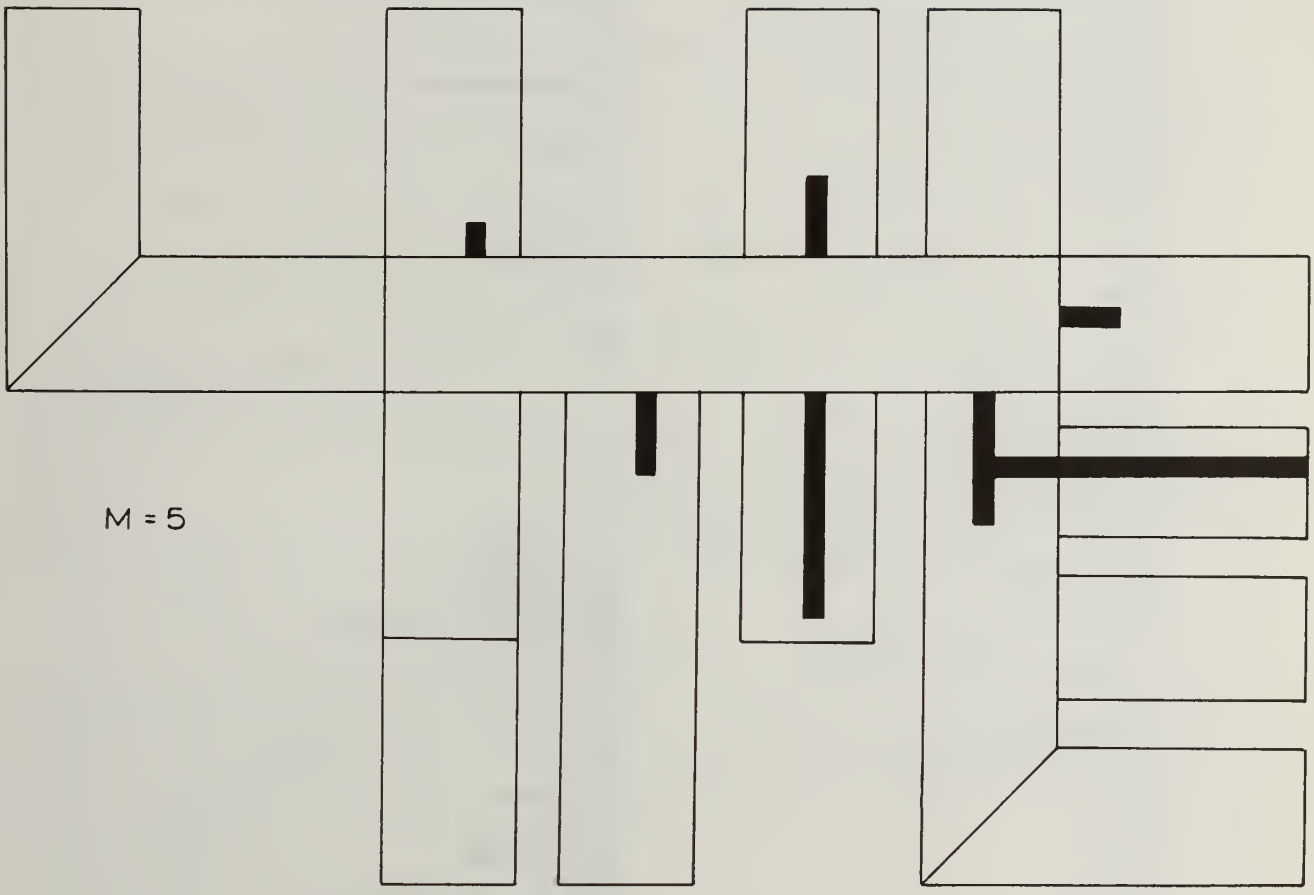


Fig. 14.6 Diagrammatic representation of the same character state as in Fig. 14.5, but assuming that it is absent from the 'centrum group' in system-II.
M = number of discontinuities.

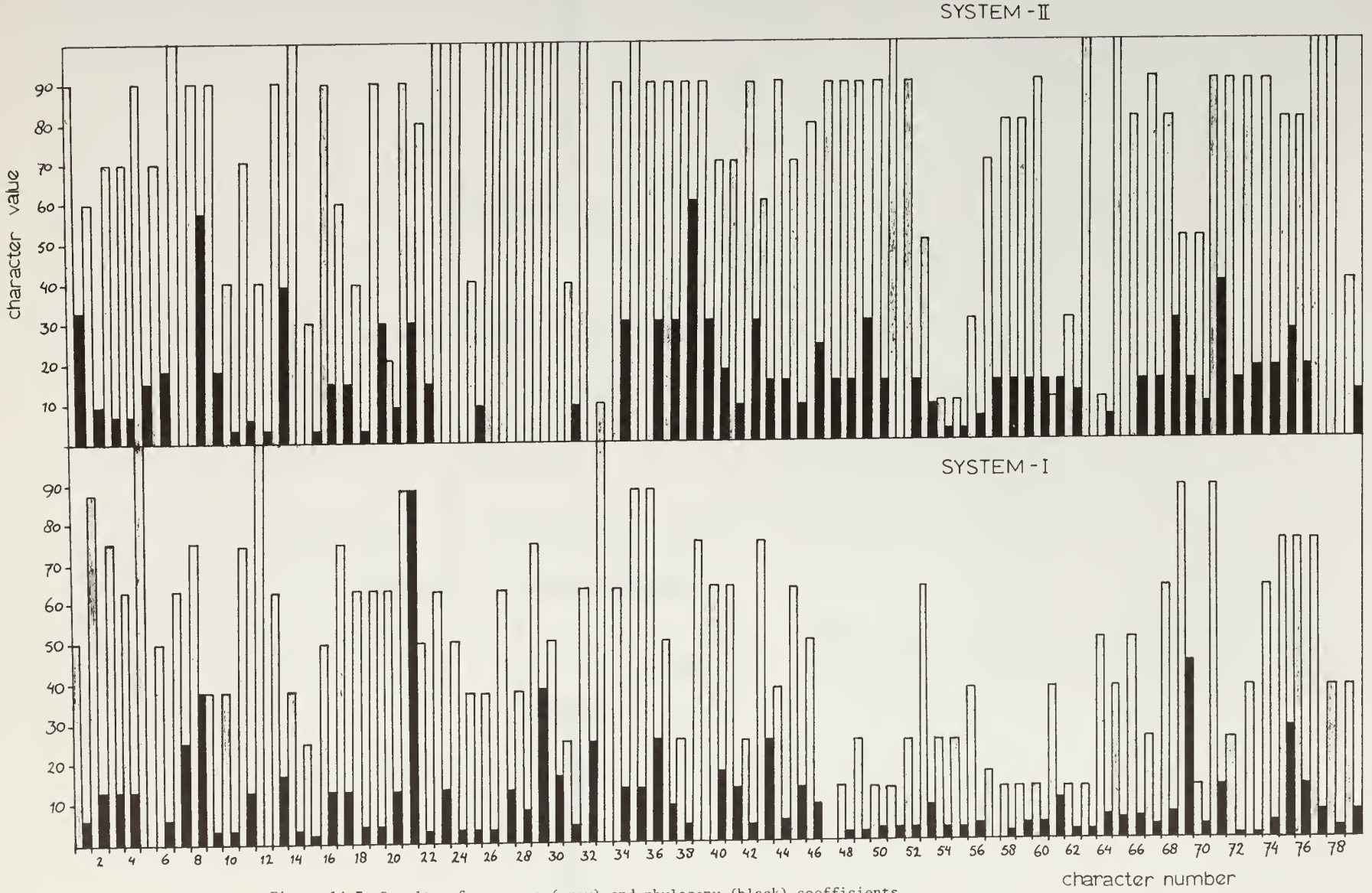


Figure 14.7 Results of sequence (grey) and phylogeny (black) coefficients of systems I and II

same distribution as the example in Fig. 14.5 but which is absent from Hypodermataceae/Phacidiaceae, is highly contradictory to that system (Fig. 14.6). Since in this system the groups have been chosen because of their possible common ancestry, the phylogenetic potential of each character should be zero.

The shape of system-II may be convenient, but it is questionable whether the choice of Hypodermataceae/Phacidiaceae as central taxon is a good one. In many cases the taxon appeared to be in a different character-state to the bordering groups, thus causing many discontinuities. In addition, many characters were also found in part of the Pseudosphaerinae and the Dothideinae, which necessarily brings in another discontinuity. Since the maximum distance between two taxa in this system is only three steps (Dothideinae - Erysiphales or Dothideinae - Ascosphaerales), this generates a considerable phylogenetic potential, thus conflicting with the above principles.

EPILOGUE

Biological classification, from Linnaeus's time onwards, has always been essentially deductive. Inductive numerical taxonomy may yield highly valuable results, but it can never fully replace this intuitive taxonomy. The purpose of the above discussions was to support classical taxonomy. When comparing systems one should not merely argue the connection of the groups, but also, or even primarily, the criteria on the basis of which one likes to order. In this way any contention between classifiers becomes more clear, and the intuitive classification becomes -- if I may arrogantly put it this way -- more scientific.

ACKNOWLEDGMENTS

I am deeply grateful to J.A. von Arx and Dave Malloch for their kind cooperation in providing me with the material which I used to work out the ideas duscussed above. I am indebted to Bryce Kendrick for valuable comments on the manuscript, to Jojada and Kitty Verrips for drawing my attention to some important literature, and to Connie van Oorschot for correction of the English text.

DIALOGUE FOLLOWING DR. DE HOOG'S PAPER

LUTTRELL: Would the purpose of these analyses be to choose between two classifications?

DE HOOG: No. the object was merely to test this deductive methodology using an actual sample.

LUTTRELL: But if you devised a classification, would you use it to test the 'goodness' of that classification? If you found it wasn't very 'good', would you then re-arrange it according to different criteria and test it again?

DE HOOG: Yes, it should help to confirm or modify your use of the various criteria available. You must, however, be sure what you are aiming for; whether for a phylogenetic scheme or something else.

LUTTRELL: Does your testing method yield any suggestions as to *how* you should modify your system?

DE HOOG: Usually you have several possible approaches in mind. It is wiser to work your way through these than to change things without having any very clear rationale for doing so.

KENDRICK: Do you intend to pursue this analysis further with Dr. von Arx and Dr. Malloch, with the aim of optimizing their schemes?

DE HOOG: Not really. I have, according to the principles I chose, shown where the areas of disagreement lie. Their two schemes are based on rather different premises. One is based mainly on similarity, one on phylogeny. One scheme is not necessarily any 'better' or 'worse' than the other. They could easily be rearranged and re-compared. It's up to Drs. von Arx and Malloch to make what they wish of the test results.

KENDRICK: You mentioned that the central position of the Phacidiales didn't seem to work out. That could be a good argument for putting another group in that position; for changing the criteria used.

DE HOOG: No doubt Dr. Malloch will reconsider this point, although it is also possible that I did not include his criteria accurately. After all, the wording of criteria, which most taxonomists apply without explicit formulation, required much discussion. I was able to ask von Arx regularly about the criteria he preferred. I didn't have as much communication with Dr. Malloch. That may be why the von Arx system seems to give a somewhat better fit.

KENDRICK: It might be fruitful to choose several different sets of criteria and compare them with one another. If the numerical taxonomists are to be believed, it should not make any difference, but I think most of us would feel that it makes a lot of difference.

DE HOOG: If one does not set any prior conditions for the required system (such as: "the taxa need to be separable by means of key-features", or "the system should express this and that evolutionary trend"), then these criteria are not needed. My method, on the contrary, is quite the opposite. In essence, one starts postulating the kind of system one wants. Therefore the system is first constructed to ensure the latter -- the ultimate classical way of making a system. The testing method is not based on the question of whether I pictured Nature correctly, but whether I reasoned logically. This testing can be carried out at random. If you take different samplings of characters, and all give a poor result, then we'd have to assume that the system was probably bad. It is not possible to base inductive classification on a sample set of characters; you would get some very strange results.

WERESUB: I didn't quite understand how you dealt with the situation in which a pseudothecium was being compared with something that might be the same thing, though now called something else. How do you get around the problem of the same thing being called by different names, and different things by the same name?

DE HOOG: That was a difficulty.

WERESUB: This is always a problem in the choice of characters. Someone who splits one character into several immediately has a set of several characters that can't be compared, one with the other, by means of the computer, whereas someone else who groups these under one name has a single character for comparison in the several taxa under study. But he, too, may be falling into a trap. Many different groups of fungi produce what is called a 'yeast phase', an analogous rather than homologous condition. Yet to the computer the

character 'yeast-like' means exactly the same thing in every case. In calling it by that name you prejudged it. What is meant to be a convenient though relatively imprecise term is used in computer analyses as if it were an absolute. In these circumstances it would seem better not to use the term 'yeast'. I wonder how many of the so-called characters you might have to throw out on that basis? For example, every time you use the word 'cystidium', the computer will assume you mean exactly the same thing. If you don't want that to happen, you'll have to distinguish between different kinds of cystidium. So this comes down to a personal judgment -- or perhaps that of a consensus of experts -- on what constitutes a character. The problems become greater when you compare things that are more and more different. As Dr. Kendrick and I discovered many years ago (Kendrick & Weresub 1966), there are many pitfalls in making numerical comparisons between high-ranking taxa like Orders and Classes.

DE HOOG: That is why characters should be broken down into subcharacters as much as possible.

KENDRICK: I like the impartiality of Dr. De Hoog's approach, but I would have more faith in the results if he were comparing genera rather than Orders. In your coding, you weren't recognizing a difference between a loculate pseudothecium and an apothecioid ascostroma.

DE HOOG: The difficulty was in drawing a sharp line between them.

KENDRICK: That seems to be one of the main problems in fungal taxonomy as a whole; there are so many intermediates. If there were too many, we couldn't construct a system at all, since we'd be looking at a continuous spectrum of variation and all our decisions would be arbitrary. Fortunately, there are enough discontinuities to allow us to erect a system that is only partly arbitrary. But we still need better bases for discriminating between groups. If we can follow Dr. De Hoog's lead by ordering our groups, then establishing taxonomic distances between the peripheral species of neighbouring groups, we may make worthwhile progress toward determining which of our groups are good. We are aiming for a system which will permit us to place *all* fungal species in appropriate larger groups. We haven't achieved it yet, and one of the questions this Conference is addressing is how we can achieve a relatively stable and acceptable level of discrimination. We believe that the characters of both teleomorphs and anamorphs must be used in an integrated way.

The next chapter, like the last, is constructed around a classificatory experiment. But there the similarity ends -- Dr. Luttrell courageously attempts to order the teleomorph by the anamorph, and demonstrates very clearly the need to approach the problem from both sides.....

15
Deuteromycetes and Their Relationships

E.S. Luttrell

INTRODUCTION

Kananaskis-I in 1969 (Kendrick 1971) was preoccupied with characters of conidiogenesis, the 'new criteria' so perceptively explored by Hughes (1953) some 16 years earlier. It was concerned with definition of these characters, with the expectation that here at last were criteria of fundamental significance on which a classification of Deuteromycetes could be based. The mood eight years later at Kananaskis-II may well be one of disillusionment. In fact, however, neither a mood of illusion nor one of disillusion is appropriate to a consideration of taxonomic characters. There is no reason to assume, in advance of testing, that characters of conidiogenesis are somehow more fundamental than, for example, characters of conidium septation. Consequently, there is no reason for discouragement if they are not.

Since 1971 emphasis has been placed on refining distinctions among types of conidiogenesis in an attempt to demonstrate their fundamentality. Nevertheless, questions concerning correlation with other characters have been raised. In a study of DNA base composition in *Humicola*, Bertoldi, Lepidi & Nuti (1973) found examples of wide ranges in GC ratios among strains of the same species or variety. For example, GC ratios in strains of *H. grisea* var. *thermoides* Cooney & Emerson varied from 42.6 to 56.9 as compared with 36.3 in a strain of *H. grisea* var. *grisea*. They concluded that strains showing great differences in DNA base composition should be recognized as distinct species, and that production of aleuriospores probably is not sufficient to define a genus. The implication is that the development of so simple a structure as an aleuriospore, which results from enlargement of a cell cut off by a septum, probably is not beyond the ontogenetic capability evolved in many diverse fungi. This argument might be extended to all conidia. If a search into the fundamental nature of the various types of conidiogenesis is carried far enough, it must arrive at a point at which development of all conidia is essentially the same: formation of a septum cutting off a cell which becomes variously differentiated. In development of a blastic (holoblastic) (Kendrick 1971) conidium, the wall layers developing above the point of septation adhere to one another. When the septum splits and releases the conidium, the split extends through the peripheral wall layer. Consequently, all of the wall layers surround the dehisced conidium. In development of a phialidic (enteroblastic) (Kendrick 1971) conidium the wall layers above the point of septation are separable. The inner layers surrounding the developing conidium burst through the separated peripheral layer, which remains intact as a basal collarette after the

septum splits to release the conidium. Electron microscopy may offer some explanation for the separation of these wall layers. If the explanation is simple, this does not alter the fact that the phenomenon occurs, nor exclude the possibility that characters based on this type of conidiogenesis may prove useful in classification. If the explanation is so complex that the repeated evolution of the phialidic type seems improbable, these characters may be assumed to have probable usefulness in separating a coherent group of Deuteromycetes. Only classification can demonstrate that the use of these characters does indeed result in the segregation of such a group. The point is that characters do not have to be fundamental. If they are useful, they are significant. If they are significant, it is nice to be able to explain why they should be significant, but the first question nevertheless is, how useful are they? This primary question of significance will be answered by classification rather than by investigations on the fundamentality of characters. The need for classification in the assessment of criteria, however, has largely been ignored. Vague mention is made of comparisons of the "new classification" with the Saccardoan system. The comparison, however, has been between unordered groupings based on conidiogenesis (blastosporae, phialosporae, porosporae) (Hughes 1953, Barron 1968) and Saccardo's groupings based on conidium septation (amerosporae, didymosporae, phragmosporae), which were used merely in arranging genera synoptically within families of Ascomycetes as well as Deuteromycetes. The question is whether a classification in which higher taxa are defined primarily on characters of conidiogenesis, would prove superior to the classification into orders and families based on conidiophore insertion and structure of conidiomata that was used by Saccardo. Only Subramanian (1962) has addressed this question in Hyphomycetes, and Sutton (1978) in the Deuteromycetes as a whole.

For the purposes of this discussion I will present an outline of a classification of Deuteromycetes integrating Hyphomycetes and Coelomycetes. This classification is based on characters of conidiogenesis, and is essentially an extension of the classification proposed by Subramanian (1962). We may then attempt to determine whether any correlations can be demonstrated between such a classification of Deuteromycetes and a classification of Ascomycetes based on ascigerous state characters. My discussion will be prefaced by notes on nomenclature and terminology.

NOMENCLATURE

Article 59 of the International Code of Botanical Nomenclature provides that in Ascomycetes and Basidiomycetes the correct name for all states of any one species is the earliest legitimate name typified by the sexual state (teleomorph). It states, however, that the provisions of Article 59 shall not be construed as preventing the use of names of imperfect states (anamorphs) and, further, that when not already available, specific or infraspecific names for anamorphs may be proposed at the time of publication of the name for a teleomorph, or later. So far as the use of binomials for anamorphs is concerned, the code is permissive. It does not require that such names be provided or used. It does not prohibit their use. Consequently, a usage of convenience has arisen, which, although possibly disturbing to orderly minds, has practical usefulness to recommend it (Luttrell 1978).

In genera such as *Botryosphaeria*, where the teleomorph is dominant, or is commonly associated with the anamorph, or follows it in a consistent and generally recognizable cycle, the

tendency is to apply the name based on the teleomorph to all states of the species. Conidial state names, if they exist, are rarely referred to. In such cases the option *not* to provide a binomial for the anamorph probably should be taken. In describing these species, however, vague and equivocal reference to the anamorph as being, for example, '*Dothiorella*-like', is inadequate. The anamorph should be identified to genus and compared with similar anamorphic species. It should be possible, for example, to refer to the '*Dothiorella* anamorph of *Botryosphaeria berengeriana*' or '*Dothiorella* anam. *Botryosphaeria berengeriana*' even if no acceptable binomial for the anamorph is available or provided. The anamorph then should be described in the same form used in describing *Dothiorella* spp. for which the teleomorph is unknown. The emphasis here is on the theoretical rather than the practical need, although both are served.

In anamorphic genera such as *Curvularia*, in which only a few species have been connected with teleomorphs in *Cochliobolus*, and these teleomorphs have been produced only in culture by mating the proper conidial strains under the proper conditions, the need for maintaining the system of nomenclature for anamorphs should be obvious. There is, for example, some lack of confidence in assigning every isolate identifiable as *Curvularia lunata* (Wakker) Boedijn to *Cochliobolus lunatus* Nelson & Haasis until a much broader background of experience with mating tests is available. It is also unreasonable to expect plant pathologists or other applied biologists to use only a daily basis 'the *Curvularia* anamorph of *Cochliobolus lunatus*' in place of '*Curvularia lunata*', however adequate the former may be for purposes of cross referencing. In this situation the preferable option is to provide an anamorphic name when a new teleomorph is described. Even in works dealing with anamorphs in which a consistent anamorphic nomenclature is desirable, however, available teleomorph names should be included. This is especially important in groups of anamorphs such as the *Cladosporium-Fusicladium* complex in which the variety of teleomorphs (*Amorphotheca, Apiosporina, Microcyclus, Mycosphaerella, Venturia*) suggests heterogeneity.

TERMINOLOGY

Terms used are indicated in the following key:

1 Spores functioning primarily as survival states ..... chlamydospores (thallospores; origin thallic)

1' Spores functioning primarily as reproductive states .....conidia ... 2

2 Conidia functioning in sexual reproduction .....spermatia (microconidia)

2 Conidia functioning in asexual reproduction, dispersal states 3

3 Conidia originating through fragmentation of hyphae or conidiophores ..... arthrospores (arthroconidia; origin arthrogenous, arthric, thallic)

3' Conidia originating as outgrowths from conidiophores 4

4 Conidia originating through apparent pores in conidiophore walls ..... porospores (poroconidia, tretoconidia; origin porogenous, tretic, poric)

4' Conidia originating as apparent extensions of conidiophore wall 5

5 Conidia originating from swelling of entire conidiophore tip ..... aleuriospores (gangliospores; origin aleuriogenous, aleuric, ganglic, murogenous, thallic)

5' Conidia originating as buds from conidiophore wall 6

6 Conidia produced singly, or sometimes synchronously when on ampullae, often developing into acropetal chains ..... blastospores (blastoconidia, botryoblastospores; origin blastogenous, blastic, holoblastic)

6' Conidia produced in basipetal chains or clusters from conidiogenous cells that remain more or less constant in length (relatively stable conidiogenous loci) or if single, from structures recognizable as phialides 7

7 Wall layers of bud forming first conidium separable; conidium breaking through outer wall whose base remains as a collarette surrounding the conidiogenous locus from which successive conidia are produced ..... phialospores (phialoconidia; origin phialogenous, phialidic, enteroblastic; conidiogenous cells phialides)

7' Wall layers of bud forming first conidium inseparable; outer wall ruptured circumscissilely at point of dehiscence, and ruptures in outer wall remaining as annellations on slight percurrent proliferations of conidiogenous cell on which successive conidia are produced ..... annellospores (annelloconidia; origin annellogenous, annellidic, holoblastic; conidiogenous cells annellides)

I am not committed to these terms. They are a matter of present convenience. Terminology is arrived at by consensus, which seems little influenced by reasoned arguments or pronouncements by individuals or committees. In the interest of avoiding a multiplicity of terms I (Luttrell 1963) proposed that conidium be used for all asexual spores in Ascomycetes and that descriptive adjectives be used when reference to conidium origin is necessary. Aleuriospore, phialospore and arthrospore, however, had a long history of usage; and porospore, blastospore, and annellospore were readily incorporated. There is a fondness for the unnecessary pycnidiospore and even the back formation to the tautological conidiospore, but the corresponding term acervulospore has never been adopted; this may be a bit of folk wisdom of taxonomic significance, suggesting that forms with acervular conidiomata should be placed in the Hyphomycetes alongside those with sporodochial conidiomata. See also the discussion of this question by Kendrick & Nag Raj in Chapter 5. The terms phialoconidium, blastoconidium, etc., are unlikely to replace the simpler terms ending in -spore; and this is just as well since, like conidiospore, they degrade the purity of conidium. Although the terms poric, blastic, and aleuric lack the rolling euphony of porogenous, blastogenous, and phialogenous, the -ic forms probably will prevail since they are consistent with the style that has been referred to as "American telegraphic" (Kendrick 1971).

I follow Subramanian (1962), Barron (1968:18, 335), and Goos (Kendrick 1971:61, 246) in distinguishing chlamydospores and conidia. It is convenient to set chlamydospores aside in a separate category, since they only cloud the issues in a discussion of conidia. On the other hand, I reject the segregation of thallospores (except as limited to chlamydospores) and conidia, and of the thallic and blastic types of conidium origin, not only because of the difficulty of maintaining the distinction based on septum formation (Hammill 1972), but more importantly because this separation obscures the need for close comparison of aleuriospores and blastospores. Elimination of thallic and blastic in this general sense permits substitution

of blastic for holoblastic. Since phialospores are perhaps the only conidia to which enteroblastic can be applied, enteroblastic can be considered a synonym of phialidic. I would, to paraphrase Subramanian (Kendrick 1971:139), restrict the terms annellidic and annellide to "the closely spaced, very regular proliferations found in the single conidiogenous cell of *Scopulariopsis, Doratomyces,* etc." since the most serious questions concern the distinctions between such structures and phialides (Carroll & Carroll 1974b, Hammill 1977, Jones 1977). The conidia in fungi such as *Sporidesmium* are aleuriospores borne on conidiophores which in some species proliferate percurrently and become annellated.

Aleuriospores should be recognized, at least for purposes of testing by classification. These are the broadly-based conidia which are essentially modifications of entire conidiophore tips, and which often are more or less indehiscent. The difficulties in arriving at a precise definition that will distinguish aleuriospores from blastospores, and that will distinguish aleuriospores borne on annellated conidiophores from annellospores, are recognized, but these difficulties should be faced. The term aleuriospore, whether appropriate or not, is justified by usage (Barron 1968). I use poric for the benefit of those who pale at porogenous. This is applied to conidia produced from 'apparent' pores in the conidiophore wall, to avoid the question of whether conidiogenesis is fundamentally different from that in the blastic type (Carroll & Carroll 1974a). The character of apparent pores is useful at some level in classification. Poric may be a barbarism, but it is questionable whether many other terms listed would stand scholarly examination.

Spermatium is used for a conidium modified for a presumed function in sexual reproduction. I use the term reluctantly, because it gives comfort to those who would derive the Ascomycetes from the Rhodophyta. The issue of Ascomycete phylogeny, however, should be considered on its merits, and terminology is no basis for determining homology. My opinion is that 'spermatia' in Ascomycetes are modified conidia, and that the term microconidia is more appropriate, although it is true that some Ascomycetes produce germinable microconidia for which no sexual function has been suggested. These spermatial states should be included in the classification of Deuteromycetes, but flagging them with the term spermatium may serve a purpose, in attracting to them the attention they deserve as a consequence of the questions of homology that have been raised. Recognition of spermatial states also may be of some value in the "botanico-anatomical" system of nomenclature proposed by Hennebert (Kendrick 1971:202-223).

CLASSIFICATION OF DEUTEROMYCETES

The class Deuteromycetes is divided into subclasses, orders, suborders, and families. Under each family is a list of representative anamorphic genera, the corresponding teleomorphic genera, and the family of the teleomorph. Families generally are those recognized in Ainsworth, Sparrow & Sussman (1973).

KEY TO DEUTEROMYCETES

1 Hyphae typically with dolipore septa, with or without clamp connections; cell walls with a lamellate structure ..... Subclass Basidiodeuteromycetidae

1' Hyphae with simple septal pores, lacking clamp connections; cell wall with an inner, electron transparent layer, and an opaque outer layer .... Subclass Ascodeuteromycetidae ... 2

2(1') Conidia produced by fragmentation of hyphae or conidiophore branches, arthrospores ..... Geotrichales

2'(1)' Conidia produced as outgrowths of conidiophores or of simple sporogenous cells 3

3(2') Conidia delicately attached to apparent pores in conidiophore wall, porospores; pores simple or surrounded by darkened rings (ringed pores must be distinguished from septal pores in conidial scars left by broad-based blastospores or dehiscent aleuriospores) .... Helminthosporiales

3'(2') Conidia attached by a more or less broad base to the conidiophore or, if delicately attached, on evident protrusions of the conidiophore wall in the form of stalks or separating cells, or on phialides 4

4(3') Conidia originating as buds with a narrow or only slightly constricted base, or on phialides 6

4'(3') Conidia originating as swellings of the entire conidiophore tip, often making the greater part of their growth after being separated from the conidiophore by a septum .. .. Bactridiales ... 5

5(4') Conidia produced singly, often dehiscent with difficulty, sometimes on percurrently proliferating conidiophores, and conidiophores then may be annellated .... Bactridiaceae

5'(4') Conidia produced in basipetal succession from relatively stable conidiogenous loci and forming chains ..... Coniosporiaceae

6(4) Conidia phialospores or annellospores produced in basipetal succession from sporogenous cells that remain constant in length ..... Melanconiales ... 10

6'(4) Conidia produced singly on the tips or sides of conidiophores or on ampullae, often forming acropetal chains ..... Moniliales ... 7

7(6') Conidiophores in pycnidial conidiomata ..... Ascochytaceae

7'(6') Conidiophores free or grouped on sporodochial or acervular conidiomata 8

8(7') Conidia developing synchronously on ampullae ..... Botrytidaceae

8'(7') Conidia not developing synchronously 9

9(8') Conidia produced in succession on tips of conidiophores that proliferate laterally between formation of successive conidia; proliferations may be clearly sympodial, or give rise to enlarged vesicles (to be distinguished from ampullae of Botrytidaceae), or both; conidia may form acropetal chains ..... Fusicladiaceae

9'(8') Conidia produced on the sides or tips of simple or variously branched conidiophores, not on successive lateral proliferations, often forming acropetal chains .... Moniliaceae

10(6) Conidia on phialides, usually in basipetal chains or heads, rarely single .... Tuberculariineae ... 12

10'(6) Conidia on annellides ..... Melanconiineae ... 11

11(10') Conidiophores free or on sporodochial or acervular conidiomata .... Melanconiaceae

11'(10') Conidiophores in pycnidial conidiomata ..... Sphaeropsidaceae

12(10) Conidiophores free or on sporodochial or acervular conidiomata .....
..... Tuberculariaceae

12'(10) Conidiophores in pycnidial conidiomata 13

13(12') Pycnidia dimidiate ..... Leptostromataceae

13'(12') Pycnidia globose or stromatic 14

14(13') Pycnidia globose ..... Phomaceae

14'(13') Pycnidia stromatic, with irregular cavities ..... Sclerophomaceae

DEUTEROMYCETES

ANAMORPH	*TELEOMORPH*	*TELEOMORPH FAMILY*
Subclass 1. Basidiodeuteromycetidae		
Spiniger	*Heterobasidion*	Polyporaceae
Subclass 2. Ascodeuteromycetidae		
Order 1. Geotrichales (arthrospores)		
Family 1. Geotrichaceae		Hemiascomycetes
Geotrichum	*Endomyces*	Endomycetaceae
		Plectomycetes
Chrysosporium	*Arthroderma*	Gymnoascaceae
Oidiodendron	*Arachniotus*	Eurotiaceae
		Loculoascomycetes
Bahusakala	*Aulographina*	Aulographaceae
Order 2. Helminthosporiales		
Family 2. Helminthosporiaceae		Pyrenomycetes
Dendryphiopsis	*Amphisphaeria*	Amphisphaeriaceae
		Loculoascomycetes
Bipolaris	*Cochliobolus*	Pleosporaceae
Curvularia	*Cochliobolus*	Pleosporaceae
Exserohilum	*Setosphaeria*	Pleosporaceae
Drechslera	*Pyrenophora*	Pleosporaceae
Dendryphion	*Pleospora*	Pleosporaceae
Stemphylium	*Pleospora*	Pleosporaceae
Alternaria	*Pleospora*	Pleosporaceae
Capnosporium	*Metacapnodium*	Capnodiaceae
Hormiokrypsis	*Ophiocapnocoma*	Capnodiaceae
Tretospora	*Balladyna (Balladynopsis)*	Parodiellinaceae
Pirozynskia	*Eupelte (Maurodothina)*	Asterinaceae
Order 3. Moniliales (blastospores)		
Family 3. Moniliaceae		Pyrenomycetes
Monilia	*Neurospora*	Sordariaceae
Oedemium	*Thaxteria*	Coronophoraceae

		Loculoascomycetes
Cladosporium	*Mycosphaerella*	Dothideaceae
Cladosporium	*Venturia*	Stigmateaceae
Periconia	*Didymosphaeria*	Pleosporaceae
Titaea	*Paranectriella*	Pleosporaceae
Helicoma	*Thaxteriella*	Pleosporaceae
Helicosporium	*Tubeufia*	Pleosporaceae
Septonema	*Mytilidion*	Hysteriaceae
		Discomycetes
Monilia	*Monilinia*	Sclerotiniaceae
Strumella	*Urnula*	Sarcosomataceae
Clavariopsis	*Corollospora*	Hyaloscphaceae

Family 4. Botrytidaceae

		Discomycetes
Botrytis	*Sclerotinia*	Sclerotiniaceae
Chromelosporium	*Peziza*	Pezizaceae
(Ostracoderma)		
Oedocephalum	*Peziza*	Pezizaceae
Oedocephalum	*Iodophanus*	Pezizaceae

Family 5. Fusicladiaceae

		Plectomycetes
Sporothrix	*Pseudeurotium*	Eurotiaceae
		Pyrenomycetes
Sporothrix	*Ceratocystis*	Ophiostomataceae
Verticicladiella	*Ceratocystis*	Ophiostomataceae
Nakataea	*Magnaporthe*	Diaporthaceae
Beltraniella	*Pseudomassaria*	Amphisphaeriaceae
Nodulisporium	*Hypoxylon*	Xylariaceae
		Loculoascomycetes
Fusicladium	*Apiosporina*	Stigmateaceae
Fusicladium	*Venturia*	Stigmateaceae
Fusicladium	*Microcyclus*	Dothideaceae
Fusicladium	*Mycosphaerella*	Dothideaceae
Heterosporium	*Mycosphaerella*	Dothideaceae
Cercospora	*Mycosphaerella*	Dothideaceae
Cercosporella	*Mycosphaerella*	Dothideaceae
Cercosporidium	*Mycosphaerella*	Dothideaceae
Passalora	*Mycosphaerella*	Dothideaceae
Ramularia	*Mycosphaerella*	Dothideaceae
Polythrincium	*Mycosphaerella*	Dothideaceae
Zygophiala	*Schizothyrium*	Schizothyriaceae
Periconiella	*Allosoma*	Englerulaceae
Chionomyces	*Melioliphila*	Pleosporaceae
Eriomycopsis	*Melioliphila*	Pleosporaceae

Tetracrium	*Podonectria*	Pleosporaceae
Pseudospiropes	*Melanomma*	Pleosporaceae
		Discomycetes
Pseudospiropes	*Strossmayeria*	Leotiaceae

Family 6. Ascochytaceae

		Pyrenomycetes
Labridella	*Griphosphaerioma*	Amphisphaeriaceae
		Loculoascomycetes
Ascochyta	*Didymella*	Pleosporaceae
Septoria	*Mycosphaerella*	Dothideaceae
Septoria	*Sphaerulina*	Dothideaceae
		Discomycetes
Digitosporium	*Crumenulopsis*	Dermateaceae
Bothrodiscus	*Ascocalyx*	Dermateaceae

Order 4. Bactridiales (aleuriospores; conidiophores sometimes annellated)

Family 7. Bactridiaceae

		Plectomycetes
Microsporon	*Nannizzia*	Gymnoascaceae
Keratinomyces	*Arthroderma*	Gymnoascaceae
Trichophyton	*Arthroderma*	Gymnoascaceae
		Loculoascomycetes
Septoidium	*Alina*	Parodiellinaceae
Septoidium	*Ophioparodia*	Parodiellinaceae
Septoidium	*Parodiellina*	Parodiellinaceae
Septoidium	*Perisporiopsis*	Parodiellinaceae
Septoidium	*Pilgeriella*	Parodiellinaceae
Clasterosporium	*Balladyna*	Parodiellinaceae
	(Balladynopsis)	
Clasterosporium	*Asterodothis*	Asterinaceae
Clasterosporium	*Clypeolella*	Asterinaceae
Sporidesmium	*Eupelte*	Asterinaceae
Triposporium	*Batistinula*	Asterinaceae
Mitteriella	*Schiffnerula*	Englerulaceae
Sarcinella	*Schiffnerula*	Englerulaceae
Sarcinella	*Neoparodia*	Parodiellinaceae
Isthmospora	*Trichothyrium*	Trichothyriaceae
Antennatula	*Euantennaria*	Capnodiaceae
Trichothallus	*Trichopeltheca*	Capnodiaceae
Acrogenospora	*Farlowiella*	Hysteriaceae
Stigmina	*Otthia*	Pleosporaceae
Spilocaea	*Venturia*	Stigmateaceae
Pollaccia	*Venturia*	Stigmateaceae

Family 8. Coniosporiaceae

		Plectomycetes
Basipetospora	*Monascus*	Monascaceae
		Pyrenomycetes
Trichothecium	*Hypomyces*	Hypocreaceae
Oidium	*Erysiphe*	Erysiphaceae
Oidiopsis	*Leveillula*	Erysiphaceae
Coniosporium	*Hysterium*	Hysteriaceae

Order 5. Melanconiales (phialospores and annellospores)

Suborder 1. Melanconiineae (annellospores)

Family 9. Melanconiaceae

		Plectomycetes
Polypaecilum	*Dactylomyces*	Thermoascaceae
		Pyrenomycetes
Scopulariopsis	*Microascus*	Melanosporaceae
Melanconium	*Melanconis*	Diaporthaceae
Stilbospora	*Prosthecium*	Diaporthaceae
Coryneum	*Pseudovalsa*	Diaporthaceae
Libertella	*Quaternaria*	Diatrypaceae
Seimatosporium	*Discostroma*	Amphisphaeriaceae
		Loculoascomycetes
Lecanosticta	*Mycosphaerella*	Dothideaceae
Prosthemium	*Pleomassaria*	Pleosporaceae
		Discomycetes
Gloeosporidiella	*Drepanopeziza*	Dermateaceae

Family 10. Sphaeropsidaceae

		Pyrenomycetes
Chondroplea	*Cryptodiaporthe*	Diaporthaceae
		Loculoascomycetes
Phyllosticta	*Guignardia*	Dothideaceae
Botryodiplodia	*Botryosphaeria*	Botryosphaeriaceae
Haplosporella	*Bagnisiella*	Botryosphaeriaceae
Haplosporella	*Otthia*	Pleosporaceae
Diplodia	*Otthia*	Pleosporaceae
Diplodia	*Eutryblidiella*	Patellariaceae
Diplodia	*Rhytidhysterium*	Patellariaceae
Fumagospora	*Capnodium*	Capnodiaceae
Phaeoxyphiella	*Capnodium*	Capnodiaceae

Suborder 2. Tuberculariineae (phialospores)

Family 11. Tuberculariaceae

		Plectomycetes
Paecilomyces	*Thermoascus*	Thermoascaceae
Paecilomyces	*Byssochlamys*	Eurotiaceae

Aspergillus	*Eurotium*	Eurotiaceae
Aspergillus	*Emericella*	Eurotiaceae
Aspergillus	*Dichlaena*	Eurotiaceae
Aspergillus	*Hemicarpenteles*	Eurotiaceae
Aspergillus	*Sartorya*	Eurotiaceae
Penicillium	*Eupenicillium*	Eurotiaceae
Penicillium	*Talaromyces*	Eurotiaceae
Penicillium	*Trichocoma*	Trichocomaceae
Acremonium	*Emericellopsis*	Pseudeurotiaceae
		Pyrenomycetes
Acremonium	*Nectria*	Hypocreaceae
Tuberculariа	*Nectria*	Hypocreaceae
Gliocladium	*Nectria*	Hypocreaceae
Heliscus	*Nectria*	Hypocreaceae
Myrothecium	*Nectria*	Hypocreaceae
Verticillium	*Nectria*	Hypocreaceae
Volutella	*Nectria*	Hypocreaceae
Fusarium	*Nectria*	Hypocreaceae
Fusarium	*Calonectria*	Hypocreaceae
Fusarium	*Gibberella*	Hypocreaceae
Stromatocrea	*Hypocreopsis*	Hypocreaceae
Trichoderma	*Hypocrea*	Hypocreaceae
Sphacelia	*Claviceps*	Clavicipitaceae
Ephelis	*Balansia*	Clavicipitaceae
Akanthomyces	*Cordyceps*	Clavicipitaceae
Chalara	*Ceratocystis*	Ophiostomataceae
Chloridium	*Chaetosphaeria*	Sphaeriaceae
Catenularia	*Chaetosphaeria*	Sphaeriaceae
Codinaea	*Chaetosphaeria*	Sphaeriaceae
Colletotrichum	*Glomerella*	Phyllachoraceae
Sporoschisma	*Melanochaeta*	Diaporthaceae
Phialophora	*Gaeumannomyces*	Diaporthaceae
Phialophora	*Coniochaeta*	Sordariaceae
		Loculoascomycetes
Sphaceloma	*Elsinoë*	Myriangiaceae
Tuberculina	*Anhellia*	Myriangiaceae
Xenodiella	*Xenodium*	Saccardinulaceae
Capnophialophora	*Limacinia*	Capnodiaceae
		Discomycetes
Phialophora	*Pyrenopeziza*	Dermateaceae
Phialophora	*Mollisia*	Dermateaceae
Phialophora	*Pseudopeziza*	Dermateaceae
Hainesia	*Discohainesia*	Dermateaceae

Myriococcum (spermatial)	*Sclerotinia*	Sclerotiniaceae
Myriococcum	*Ciboria*	Sclerotiniaceae
Myriococcum	*Rutstroemia*	Sclerotiniaceae
Family 12. Phomaceae		
		Pyrenomycetes
Phomopsis	*Diaporthe*	Diaporthaceae
Zythia	*Gnomonia*	Diaporthaceae
Discula	*Gnomonia*	Diaporthaceae
Discula	*Apiognomonia*	Diaporthaceae
Rabenhorstia	*Hercospora*	Diaporthaceae
		Loculoascomycetes
Selenophoma	*Guignardia*	Dothideaceae
Phoma	*Didymella*	Pleosporaceae
Darluca	*Eudarluca*	Pleosporaceae
Coniothyrium	*Paraphaeosphaeria*	Pleosporaceae
Coniothyrium	*Massarina*	Pleosporaceae
Pyrenochaeta	*Herpotrichia*	Pleosporaceae
Pyrenochaeta	*Cucurbitaria*	Pleosporaceae
Microsphaeropsis (spermatial)	*Massarina*	Pleosporaceae
Asteromella (spermatial)	*Mycosphaerella*	Dothideaceae
Asteromellopsis (spermatial)	*Dothidea*	Dothideaceae
		Discomycetes
Phacidiopycnis	*Potebniamyces*	Cryptomycetaceae
Family 13. Sclerophomaceae		
		Pyrenomycetes
Cytospora	*Leucostoma (Valsella)*	Diaporthaceae
		Loculoascomycetes
Sclerophoma (Dothichiza)	*Dothiora*	Dothideaceae
Sclerophoma	*Sydowia*	Dothideaceae
Colletotrichella	*Guignardia*	Dothideaceae
Sarcophoma	*Guignardia*	Dothideaceae
Scleroparodia	*Parodiella*	Pleosporaceae
		Discomycetes
Micropera	*Dermea*	Dermateaceae
Pleurophomella	*Tympanis*	Leotiaceae
Brunchorstia	*Scleroderris*	Leotiaceae

Family 14. Leptostromataceae

		Loculoascomycetes
Leptothyrium	*Leptopeltopsis*	Leptopeltaceae

CONCLUSIONS

The Basidiodeuteromycetidae have been given only token consideration since they are treated in detail by Kendrick & Watling in Chapter 20. It need only be noted that characters derived from septation (presence or absence of clamp connections) and septal pores (dolipores or simple pores) furnish a basis for a major division of Deuteromycetes into Ascodeuteromycetidae and Basidiodeuteromycetidae, and there are possibilities that this basis may be broadened by characters derived from wall structure (Bronchart & Demoulin 1975) and biochemistry. Also, significant generalizations on major types of conidiogenesis characterizing the Basidiodeuteromycetidae have been developed by Kendrick & Watling (Chapter 20). The difficulty, of course, is that although characters such as nature of septal pores may be dependable in classification, they are not convenient characters for identification. The answer is that once the classification is established, correlated characters more useful for purposes of identification may be found. This is illustrated by Stalpers's (1974a,b) work on *Oedocephalum*. Although *Oedocephalum* was established for anamorphs of *Peziza*, other fungi, among them anamorphs of Basidiomycetes, were added to the genus. With the knowledge that the *Oedocephalum* complex comprised disparate elements, Stalpers found simple characters of conidia and conidiophores that could be used to distinguish basidiomycetous components as the genus *Spiniger*. Although Stalpers's work started from knowledge of teleomorph relationships, in the absence of this knowledge it could have proceeded as well from septal pore structure. Hanlin (1978) has demonstrated the presence of dolipore septa in *Spiniger meineckellus* (A.J. Olson) Stalpers [= *Oedocephalum meineckellum* (A.J. Olson) Donk].

The more extensive treatment of the Ascodeuteromycetidae is an Adansonian exercise in which Deuteromycetes with reported ascomycetous teleomorphs are classified in a system based primarily on characters of conidiogenesis. The only test applied to this system is its goodness of fit with a classification of the teleomorphs. Although the focus is on testing the classification of Deuteromycetes that has been set up for this purpose, the classification of Ascomycetes employed is open to question, and this likewise is tested. Questions concerning the effects of anamorphs on the classification of Ascomycetes, however, are considered elsewhere in this book. Finally, the facts on which the classifications are based are also subject to testing (Luttrell 1977).

A glance at the genera and their teleomorph connections listed under the families of Ascodeuteromycetidae is sufficient to indicate that this classification has not met the test with conspicuous success. Teleomorphs of the genera in most families and orders are distributed over the major groupings of Ascomycetes: Pyrenomycetes, Discomycetes, and Loculoascomycetes. The integrated classification of Hyphomycetes and Coelomycetes, in fact, raises questions concerning previously suggested correlations between teleomorphs and groupings of Hyphomycetes based on type of conidiogenesis.

In the Tuberculariaceae the preponderance of teleomorph connections with the Eurotiaceae, Hypocreaceae, and Clavicipitaceae supports Tubaki's (1958) generalization on the association

of phialidic Hyphomycetes with these groups of Ascomycetes. The association of the acervular phialidic states *Sphaceloma*, *Tuberculina*, and *Xenodiella* with the teleomorphs *Elsinoë*, *Anhellia*, and *Xenodium* in the Loculoascomycetes can only be noted as an oddity. Extension of consideration to the Phomaceae (Coelomycetes), however, has the diluting effect of increasing the number of phialidic forms connected with other families of Pyrenomycetes, such as the Diaporthaceae, and with families of Loculoascomycetes. Some of the genera in the Phomaceae, such as *Asteromella* and *Asteromellopsis*, are certainly spermatial states, and this may be true also of many other genera. If genera representing spermatial or accessory microconidial states were excluded, exceptions to the correlation between phialidic anamorphs and teleomorphs in the Eurotiaceae-Hypocreaceae-Clavicipitaceae might be reduced to the extent that a reexamination of the apparent exceptions would be in order. On the other hand, if spermatial states are taken into consideration, the lists of genera inadequately reflect the occurrence of phialidic states throughout the Ascomycetes, since these states frequently are not assigned to genera. Similarly, any attempt to discover a possible association of annellidic anamorphs in the Melanconiaceae with Pyrenomycetous teleomorphs is disrupted if consideration is extended to the annellidic Coelomycetes in the Sphaeropsidaceae. Most of the teleomorph connections in the Sphaeropsidaceae are with Loculoascomycetes.

Recognition of the aleuric type of conidiogenesis, and its use in defining the Bactridaceae, accomplishes approximately the same level of correlation with teleomorphs as that attained in the Tuberculariaceae. The majority of teleomorph connections in the Bactridiaceae are with the Parodiellinaceae, Englerulaceae, Asterinaceae, and Trichothyriaceae. These are families of Loculoascomycetes growing as superficial parasites of plants. Formation of aleuriospores might be a response to the superficial habit of these fungi, although the specialized function aleuriospores might perform in this environment is obscure. Certainly, if it is a response to the superficial habit, it is no more a necessary response than the dimidiate structure of the ascoma found in the Asterinaceae but not in the other ecologically similar families. Occurrence of aleuriospores in Gymnoascaceae disturbs this correlation. Designation of conidiogenesis in *Stigmina*, *Spilocaea*, and *Pollaccia* as aleuric may be a misinterpretation, as suggested by the difference in teleomorph connections. However, interpretation of their conidiophores as annellides would place them in the Melanconiaceae, where they would be no less disruptive. Finally, teleomorph connections indicate that interpretation of conidiogenesis in *Basipetospora*, *Trichothecium*, *Oidium*, and *Oidiopsis* as meristem aleuric and placement of these genera in the Coniosporiaceae is incorrect. These genera had been better left in the Geotrichales.

The Helminthosporiaceae may be a coherent group. Müller (1971) indicated that forms with poric conidiogenesis are connected with teleomorphs in the Loculoascomycetes. Hughes (1972) suggested more specifically that production of porospores is correlated with the *Pleospora*-type centrum in the teleomorph, and used poric conidiogenesis in the anamorphs *Capnosporium* and *Hormiokrypsis* as a supplementary character in separating the Metacapnodiaceae from the Capnodiaceae, and placing the Metacapnodiaceae in the Pleosporales. The Helminthosporiaceae, however, like the Botrytidaceae, in which all genera have teleomorphs in the Discomycetes, is a small family containing only a few genera. Even so, *Dendryphiopsis*, with a teleomorph reported in the Pyrenomycetes *(Amphisphaeria)*, is an apparent exception. On one point

classification seems instructive in questioning facts. *Tretospora* and *Pirozynskia*, with teleomorphs in the Parodiellinaceae and Asterinaceae, are obvious misfits. The Parodiellinaceae and Asterinaceae otherwise have anamorphs in the Bactridiaceae. Ellis's (1976) illustrations are sufficient to indicate that conidiogenesis in *Tretospora* is not poric. The conidia are aleuriospores in which the hilum is formed by a thickened septum perforated by a septal spore. *Tretospora*, even if it is distinct from *Clasterosporium*, belongs near *Clasterosporium* in the Bactridiaceae. On the other hand, there is nothing in the illustrations of *Pirozynskia* by either Ellis (1976) or Pirozynski & Shoemaker (1970) to suggest that conidiogenesis is not poric, as it has been described.

An attempt to develop a satisfactory hierarchical classification of Deuteromycetes would constitute a theoretical contribution to the ultimate goal of producing an integrated classification based on holomorphs. A reliable major division into Ascodeuteromycetidae and Basidiodeuteromycetidae, which seems within reach, would overcome the major hurdle, and would suggest that a useful classification of taxa in lower categories is attainable. A general system of classification incorporating and organizing data from applied as well as theoretical sciences also is an immediate practical necessity (Luttrell 1978). That a system based exclusively on characters of conidiogenesis should prove to be inadequate in meeting one of the major goals of such a classification, that of predicting probable teleomorphs, is hardly unexpected. There is, however, sufficient encouragement from the limited information obtained from this test to indicate that conidiogenesis does furnish additional morphological characters that, in combination with all other available characters, may be used to develop the general system needed.

DIALOGUE FOLLOWING DR. LUTTRELL'S PAPER

PIROZYNSKI: Would you perhaps prefer to treat the genera of Deuteromycetes as natural genera, to compete on an equal footing with any others?

LUTTRELL: This is a practical necessity. I would approach it in two steps. We should first devise a hierarchical system of classification for the Deuteromycetes. This need not raise any major problems, since even a mail-order catalogue is arranged like that. A classification is necessary, but it doesn't imply anything profound. There may be a few minor problems. Where do you put these socks that have slippers sewn onto the feet -- in hosiery or in shoes? But such small difficulties needn't disturb us. The second step would be more difficult, but when people say that it's obviously impossible to produce a natural system for the Deuteromycetes it grates on my nerves. It may be 'impossible' meaning that it will take a little longer to do. But to say it is obviously impossible means that you should not even try. And we obviously are trying. The obvious assumption here is that we are capable of producing a natural system for the teleomorphs of Ascomycetes and Basidiomycetes, but perhaps this is impossible also. It seems to have become axiomatic that if we have a sexual state -- a teleomorph -- we *can* do it, but if we have an anamorph we can't do it, and we must not even try. I disagree. I don't even like to

call anamorphic taxa 'form taxa', because this term really applies to the fossil fungi.

PIROZYNSKI: It is, perhaps, not so much the question of whether it is possible to classify anamorphs in a "natural" system, but whether it is desirable.

As for form-taxa of fossils I presume the term was originally intended to describe an entity with insufficient characteristics to relate it to a modern taxon. Our 'form-taxon' is an anamorphic taxon, i.e., an asexual uncorrelated phase in a life cycle or an autonomous pseudo-species. I agree that the two concepts are not mutually exclusive because the incompleteness is of a different kind. A fossilized conidium is a fossil form-taxon of an anamorphic 'form-taxon'. To avoid confusion we should perhaps replace 'form-taxon' in living fungi by 'anamorphic taxon'.

LUTTRELL: Ideally, we must proceed with the classification of holomorphs, but in the meantime we must do as much as we can with the anamorphs. People will ask: "I have this anamorph: can you guess what the teleomorph might be? What shall I look for? Where shall I look?" They want us to be able to predict. Our classification should be aimed at answering such questions.

WATLING: I began corresponding with Bryce in about 1970, and we have since exchanged innumerable letters, because I thought that there might be a way in which the anamorphs of Basidiomycetes could be fitted in with those of the Ascomycetes so that we wouldn't need to produce yet another set of descriptive terms. This works much of the time, but there is at least one snag. I was under the impression that the term chlamydospore was defined by de Bary for a very special kind of spore in *Nyctalis*, which is definitely a dispersal spore, not simply a survival mechanism.

LUTTRELL: [*sotto voce*] I think we need a new term for that!

WATLING: In your key you eliminate spermatia at an early stage, but in the Basidiomycetes the arthric conidia, more often than not, act as spermatia.

WEBSTER: Could we get this term straight? I think it is wrong to equate microconidia with spermatia. If they function solely in sexual reproduction you can call them spermatia. If they can also germinate, you may call them microconidia. A spermatium is not capable of independent germination -- it functions only in a sexual context.

KENDRICK: Yes. I use spermatium as a general term for a non-motile male cell (gamete), and these may occur in very diverse groups, for example, the red algae, as well as Fungi like the Uredinales.

LUTTRELL: I was using microconidia to get away from the association with the red algae that might be inferred from the use of 'spermatia'.

KENDRICK: I don't think that's the way to do it. We shouldn't have a different term for what is essentially the same structure in different groups. We would finish up with an enormous number of obligate or facultative synonyms, to use the terminology of nomenclature. A meiospore, for example, is a meiospore, no matter which group of organisms produces it. It's important to stress similarities as well as differences. We are, after all, seeking underlying generalizations in science, and we won't find them by always stressing differences.

SUBRAMANIAN: I have long felt that there are only five basic types of conidia -- the arthrospore, the aleuriospore, the blastospore, the porospore, and the phialospore, whatever

that means, for the phialospore is a different thing in different fungi, and we may yet learn more about it as we go on.

I'd also like to point out that the annellide and the phialide are now considered to be very close to one another, and it is very difficult if not impossible to draw a clear dividing line between them with the light microscope.

VON ARX: Following the publication of the book arising from the first Kananaskis Conference (Kendrick 1971) we at Baarn sat down and discussed it for several afternoons. We came to the conclusion that most of the new proposals had to be accepted. But we did not agree with the distinction between enteroblastic and holoblastic development because we could not understand why the tretic, or poroconidia, should be in the same major grouping as the phialidic conidia. So we use the terms blastic or thallic as the 'prefix' for terms describing more specialized aspects, such as whether a plurality of conidia is formed synchronously, or sympodially, or in acropetal or basipetal chains. So we did not use the terms annellidic and phialidic -- and now it seems we were justified in this, because the EM has shown that there is a complete intergrading series between what are called phialides and what are called annellides. So the conidium/conidiogenous cell classification has been simplified and is easier to use.

KENDRICK: I don't quite know how to reply to the trend that has emerged in the last few minutes, except to say that everyone takes from a book like 'Taxonomy of Fungi Imperfecti' exactly what he wants -- he uses what he finds acceptable, and he rejects what he can't swallow. It has become apparent that at Kananaskis-I we separated a number of things that are now known to be less distinct than we thought then -- cases in which we now recognize many intermediate forms. We considered the biological continuum as a sort of monilioid hypha, and tended to accentuate the broad bits and minimize the narrower parts that lay between them. We drew some rather arbitrary lines delimiting the large chunks -- the more frequently encountered kinds of conidiogenesis. We did mention the mavericks, *Chloridium (Bisporomyces) chlamydosporis* and the like, but we downplayed them. Now the more fungi you look at, the more of these mavericks you will find. But even now that we have seen how these fit into the continuum, it still seems to me that the oddballs are valuable as indicators of linkage rather than of a hidden iceberg of similar forms. Thus even though we know that the 'phialide' and the 'annellide' are closely related (I think related is the right word), we can still in many cases distinguish a conidiogenous cell that elongates during conidiogenesis, accumulating annular scars as it does so, from one that doesn't elongate, and accumulates its extra wall layers internally. If we can *see* the difference we can certainly use it in classification, provided it always behaves the same way. And of course examples exist which *are* mutable. Mrs. Wang shows us some of these in Chapter 7 and Dr. Madelin provides an elegant hypothesis to explain them in Chapter 6.

I will restate the point with which I began: terms are ultimately accepted or rejected not by the will of one person, or one Conference, but by the mycological community as a whole over a period of many years. It is still too early to say when or in what form the terminology of conidiogenesis will solidify. But I still believe that an analytical multiple-adjective terminology, such as I have long advocated, is the most flexible and

adaptable kind. The terms are handles by which we try to grasp and communicate concepts. If our ideas change, and the handle no longer fits, we look around for a new and better-fitting one.

The last point I want to make is that we must now surely realise that the dream of a 'natural' classification of Fungi Imperfecti based exclusively on conidiogenesis has evaporated. We must now simply accept information about conidiogenesis as taxonomically useful data, on a par with many other kinds of data. If conidium ontogeny is useful in one area, let's apply it; if conidiophore structure is helpful in another area, let's use it; if pigment or septation work in other examples, let's adopt them.

LUTTRELL: It doesn't matter if the system we come up with is rather artificial at first, as long as it works. We must make the attempt.

VON ARX: In our recent papers, Dr. Müller and I have been able to circumscribe what we believe to be 'natural' genera, but we have had to construct rather artificial families. We believe that when the anamorphs are taken account of in the classification of the bitunicates, more natural taxa will emerge.

WERESUB: It seems to me that we must distinguish between the anatomical system of naming anamorphs and an artificial classification of fungi. When I started in mycology, I learned about two very closely related genera, *Corticium* and *Peniophora*, distinguished by the presence of cystidia in the genus *Peniophora*. This was certainly an artificial classification, but the nomenclatural system was a botanical one. In the anatomical system that we use for anamorphs, form-genera like *Uredo* may be as natural as *Puccinia* which is a true genus in the botanical system. But as long as the so-called species of *Uredo* are accepted as anatomical entities of species of *Puccinia*, the naturalness of *Uredo* does not make it any less a form-genus. Donk made the point that anamorphic taxa are 'pseudogenera' and 'pseudospecies'. If you adopt a schizoid approach to anamorphic taxa, treating them simultaneously both as true taxa and as pseudotaxa that are parts of other true taxa, indeed if you drop the distinction between form-taxa and true taxa, you are bound to get into a state of complete confusion.

LUTTRELL: I've dropped it.

WERESUB: And you don't think you are going to get into a state of confusion?

LUTTRELL: Oh, I've been that way.

KENDRICK: One of the purposes of this meeting is to reduce, however marginally, this state of confusion. One way in which we can achieve this is by discriminating between those conidial states (anamorphs) that are conservative -- reasonably stable in their configurations -- and therefore taxonomically useful; and those that behave in the manner Dr. Madelin described -- a 'treacherous and mutable tribe' -- and are taxonomically unreliable. I hope this kind of thing will show up in the lists of connections, and their accompanying commentaries, which will form an integral part of the book arising from the conference.

CARMICHAEL: Would somebody please define what they mean by a 'natural' system?

MADELIN: It will have a high information content and, consequently, high predictive value and phylogenetic implications.

KENDRICK: This is why a lot of our developmental information in anamorphic fungi is of no use in terms of a 'natural' system because it does *not* have predictive value. The same

mechanism of conidium ontogeny has in all probability been evolved over and over again. Even the phialide may have evolved more than once. The phialides of *Chalara* and *Penicillium* look and behave rather differently.

LUTTRELL: I'm not sure they are the same thing.

KENDRICK: Exactly: we call them both phialides because they both produce a basipetal sequence of blastic conidia without becoming longer or shorter, but they may not necessarily have evolved from the same ancestor. It's even more obvious that the sympodial mechanism has evolved many times. In our compilation of Basidiomycete anamorphs (Chap. 20), Roy Watling and I grouped those exhibiting sympodial proliferation simply as a matter of convenience and to follow an established protocol. But a more diverse bunch would be hard to find. Obviously they aren't closely related by descent.

WERESUB: Is it not perfectly legitimate to use a term such as phialide for a particular mode of conidiogenesis without worrying about its phylogenetic implications?

KENDRICK: But we assume that it has phylogenetic implications when we use it as the mainstay of a classification which we hope to be natural.

WATLING: And Kananaskis-II suggests that we shouldn't.

MÜLLER: In 1969 we were already aware that these terms did not imply phylogenetic relationship. We merely wanted names for similar structures so that we could have a common language. I think this was stated quite clearly. In my Table 13.1 (Taxonomy of Fungi Imperfecti, p. 186) the different kinds of conidiogenesis found in each Ascomycete group are compiled. It is obvious that phialides occur in most orders of Ascomycetes, and could not be used to establish natural groups.

KENDRICK: This is a myth that dies hard. Stan Hughes voiced a hope in 1953 that developmental features would help in establishing a natural system. Soon this hope became dogma in the minds of the faithful, and we are now having a hard time dislodging this 'idée fixe'. Of course developmental information is useful -- but not more so than many other kinds of data. We need them all.

CARMICHAEL: I'd like to clarify two terms which seem to be causing some confusion. The first is 'natural' system. By this I mean a system based on all the information we have about the things to be classified. An artificial system of classification is based on some selected characters of the things to be classified. So it is absolutely impossible to make a natural classification of fungi based only on anamorphs. The second confused term is 'related'. Things may be related by descent, (lineage, ancestry) -- phylogenetic relationship. But things may also be related by function. This kind of relationship may be an expression of phylogenetic relationship, or it may have no such implications whatsoever. Thus certain anamorphs may all have blastic-sympodial development but this need not imply any phylogenetic relationship (and conversely, organisms related by descent may not share functional relationships). So we must qualify this word 'related' by another word -- 'phylogenetically' or 'functionally'.

KENDRICK: As a logical corollary of those remarks, it is equally impossible to produce a natural classification of the fungi using only the teleomorphs.

CARMICHAEL: That's right. The natural system by my definition uses *all* of the available information.

VON ARX: And not only morphology, but chemistry and anything else that is known.

PIROZYNSKI: We should start by curing ourselves of the schizophrenia of the dualistic approach. What we need is a system for *holomorphs*. We are depriving ourselves of 50% of the potential information if we accept a 'natural' system for anamorphs separately from that for teleomorphs, i.e., if we consider only halves of the organisms.

KENDRICK: And we are here to try and bring the two halves together. Our lists of connections are good raw material for your expert scrutiny.

DICOSMO: These lists took several people a long time to compile, but they can be only as useful as the literature they are derived from. There are many inconsistencies in that literature. In 1972 Barr suggested that *Lecanosticta* is closely similar to *Septoria*, but as far as we at Waterloo can tell, the two genera are quite distinct. The teleomorph was given as *Scirrhia acicola*.

VON ARX: That is a *Mycosphaerella*.

DICOSMO: That is just the point. We must agree on the taxonomy of both the teleomorphs and the anamorphs, before we can hope to integrate them properly.

KENDRICK: Unfortunately, of the names you just mentioned, I believe that *Mycosphaerella* and *Septoria* are 'aggregates' or, to put it more crudely, catch-alls.

NAG RAJ: *Septoria* is a large and rather heterogeneous genus, with 400 species, and three different kinds of conidiogenesis -- blastic-sympodial, blastic-solitary, and phialidic. We don't know what the type species is.

VON ARX: *Septoria* is natural insofar as it represents the anamorph of *Mycosphaerella*! We must try to make the generic concepts of anamorphs as natural as possible. Many form-genera contain anamorphs of both Ascomycetes and Basidiomycetes. I think this is wrong: these ought always to be in different taxa, no matter how morphologically similar they are. But we can usually tell the difference once we suspect it -- of course it's easy if there are clamps, or dolipores; and Basidiomycetes have xylose in the cell walls, which is *not* found in Ascomycetes.

WERESUB: Perhaps what is needed is to *retain* the anatomical character of anamorphic genera as long as this is useful. Even if they fit into holomorphic groups, they can still be useful as form-genera.

KENDRICK: Fortunately, as Roy Watling and I have found, there is not a tremendous amount of overlap, since the kinds of conidiogenesis favoured by the two great groups are usually different. 'Phialides' (whatever they are) are commong among Ascomycetes, rare in Basidiomycetes: thallic-arthric ontogeny is common among Basidiomycetes, much less so among Ascomycetes. But even where there is overlap we've made a lot of progress. Stalpers (1974) has shown how the ascomycetous anamorph *Oedocephalum* can be distinguished from its segregate, the basidiomycetous anamorph , *Spiniger*; and Sigler & Carmichael (1975) have made a start on separating thallic-arthric anamorphs of Ascomycetes and Basidiomycetes.

VON ARX: I have a question for Dr. Luttrell. You list the anamorphic genera *Bipolaris, Drechslera, Curvularia* and *Exserohilum*. Subramanian and also Ellis regarded *Bipolaris* as a synonym of *Drechslera*. My own feeling is that *Bipolaris* should be a synonym, not of *Drechslera*, but of *Curvularia*. I cannot use the difference between euseptation and distoseptation as a generic criterion, because that leads to the formation of unnatural taxa.

LUTTRELL: Yes, if we look at the list of connections, we see that both *Bipolaris* and *Curvularia* are given as anamorphs of *Cochliobolus*. When we find two very similar anamorphic genera connected to a single teleomorphic genus, then you may suspect that the distinctions between the anamorphic genera are unnatural. Yes, I think *Bipolaris* probably should be a synonym of *Curvularia*. This is the kind of refinement that the list of connections may be able to guide us toward. But I do hope that if someone does this that it will not be simply by taking every species of *Bipolaris* ever described and making a new combination in *Curvularia* for it without examining it first. Some problems with nomenclature might be straightened out. For example, the first name provided for the sugarcane eyespot fungus was *Cercospora sacchari* Breda de Hann (1892). The epithet *sacchari* was pre-empted in *Helminthosporium* by *H. sacchari* Butl. in Butl. & Hafiz (1913), a probable synonym, in *Bipolaris* by *B. sacchari* (Butl. in Butl. & Hafiz) Shoemaker (1959), and in *Drechslera* by *D. sacchari* (Butl. in Butl. & Hafiz) Subramanian & Jain (1966). Breda de Haan's *Cercospora sacchari* could be rescued by transfer to another genus. This opportunity has already been missed twice.

MÜLLER: *Bipolaris* conidia germinate only from each end, while *Drechslera* conidia can germinate from all cells of the phragmoconidium.

LUTTRELL: This is one area in which feedback has gone on in both directions. The taxonomy of the anamorphs has been modified by what is known about the teleomorphs. And I think the taxonomy of the teleomorphs has been affected by what is known about the anamorphs. This is as it should be. We may seem to be going in circles, but we are in fact using all the available information.

When you use the term phialide, you may be using a term that describes analogous structures (similar structure and function, different origins -- 'related' by form or function) rather than homologous structures (common origin -- related by descent). There may be many kinds of phialide with different origins. If you find two rather different groups of Ascomycetes that both produce phialides, then you should re-examine and compare the phialides very carefully, because they may in fact, despite great similarity, be analogues rather than homologues.

KENDRICK: Phialides are common in the Hypocreales, and also in the Eurotiales. I don't know how closely they are 'related', and perhaps Dr. Malloch will tell us.

MALLOCH: You may be overemphasizing the differences between phialides, because it is fashionable nowadays to attribute many similarities to parallel or convergent evolution. But consider the ascus. Surely asci would not be considered to have different origins just because they look different? The phialide may well have originated once -- it is widespread throughout the Ascomycetes. I find it hard to imagine its evolving over and over again and converging from so many different starting points.

WERESUB: We keep coming back to the same question: are all the conidiophores that are called phialides necessarily the same structure?

MALLOCH: I think they are nearly as basic to the Ascomycetes as the ascus. Despite differences in size and shape, the mechanism of conidiogenesis is very uniform. It's not hard to imagine their evolving all these different morphologies from a basic pattern.

MADELIN: I suspect that on mechanical grounds there may be two different sorts of phialide: the *Chalara*-type in which growth takes place in the side-walls, and the *Aspergillus*-type, where growth occurs in a transverse septum.

MALLOCH: Is this a really profound difference that would have been maintained throughout the ages, or something that could have evolved fairly quickly?

KENDRICK: The strange process we recorded by time-lapse photomicrography in *Chalara* may be just a response to the withdrawal of the conidiogenous locus to a position deep within the conidiogenous cell.

LUTTRELL: You are making me nervous, because the character on which *Exserohilum* is based, and which is correlated with the *Setosphaeria* teleomorph, is the protuberant hilum at the base of the conidium. This is not a very conspicuous or impressive character. How significant is it? It *has* had considerable predictive value. In some species of *Bipolaris* which have a flat hilum, the teleomorph turned out to be *Cochliobolus*. After half a dozen such cases, I began to use the presence of a flat hilum to predict what the generic identity of the teleomorph would be. In *Curvularia*, the same thing happened -- a flat hilum meant a *Cochliobolus* teleomorph. This suggested to me that the other characters like curvature of the conidium are not important, and that *Curvularia* with a flat hilum was the same as *Bipolaris* with a flat hilum. What about *Curvularia* with a protuberant hilum? Would it be correlated with a *Setosphaeria* teleomorph? It was a *Cochliobolus* again. My conclusion (Luttrell 1977) is that the so-called protuberant hilum in *Curvularia* is something different from that found in *Exserohilum*. The thing in *Curvularia* may actually be a small appendiculate cell. I'm a little uncomfortable about my reasons for reinterpreting this structure, but I'm sure that's the way we must work. The question that presents itself now is: why does the protuberant hilum of *Exserohilum* predict the teleomorph, while the appendiculate cell in *Curvularia* predicts nothing? This is linked to the idea of the cryptic species in zoology. You find two populations that you consider to be identical in every respect, yet they will not interbreed. If you re-examine these populations more closely, you will usually come up with differences that you missed the first time around. Perhaps in the fungi we also have cryptic characters. Whenever there is a difference in pathogenicity the question arises: can you tell the difference between the organisms? They behave differently; so let's find some morphological way of recognizing the different entities. We may be open to an accusation of circular reasoning but I think we have no alternative.

KENDRICK: Perhaps we can reply to such charges by saying that what we are doing is simply applying the principle of feedback.

DE HOOG: I think two things have become mixed up here. In one case you have something that exists -- a character. In the other case, you have something you make up, or conceive -- a classification. In the latter case you can have circular reasoning, but in the former you would call it searching for correlation of characters, which is a good thing.

KENDRICK: It isn't valid to manipulate the characters to suit a particular point of view, but it is always OK to re-examine them.

PIROZYNSKI: In pleomorphic Ascomycetes we should use characters of anamorphs to evaluate the "taxonomic weight" of characters of teleomorphs and vice versa. Means of independent,

objective assessment are especially useful in reappraisal of weakly characterized 'borderline' groups, because it is not necessarily the most obvious character that is most significant.

MALLOCH: Can you define 'form' taxa on any basis other than their form? If you are taking your cue from characters of the teleomorphs, then they are no longer 'form taxa', but rather part of botanical taxa. That might be desirable, but would be premature at present.

LUTTRELL: What if I am classifying a fungus which, though known only by its anamorph, has been so intensively worked on that a vast body of information has been accumulated -- biochemical, physiological, morphological, ecological. Yet this is not supposed to be acceptable as a botanical taxon, and I can't use it to establish a 'natural' classification. On the other hand, you may have someone who merely looks at a few herbarium specimens of teleomorphs, does not know the rest of the life cycle -- in fact knows very little about the organism -- yet he is supposed to be establishing a 'natural' classification, simply because he happens to have the sexual apparatus. This is unjust and unacceptable. If I can't set up a 'natural' classification, despite the fact that I have a hundred times more information than he has, then I don't believe his classification is natural either. I don't want to be the only one that is unnatural.

KENDRICK: I think we have already said something like that: a natural system can ultimately be based only on the holomorphs.

LUTTRELL: But mycologists have been talking for a hundred years about a 'natural' classification based entirely on teleomorphs.

KENDRICK: Yes, that's why we have rejected the phrase 'perfect state' in favour of the term 'holomorph', and the sexual state is designated specifically by the term 'teleomorph'.

LUTTRELL: But we have comprehensive information on the holomorph for only a few hundred out of perhaps a million living fungi. Everything else is still in limbo.

KENDRICK: It's very important to realize how superficial our acquaintance with the fungi is. But statistics show us that you don't need to sample an entire population to get a valid picture of what's going on. You yourself, working with a few organisms (and very important ones they are), have produced a very nice scheme of anamorph-teleomorph correlations.

LUTTRELL: But I am still amazed at how little we know, and how much there is still to find out. Just think what is implied in that little word 'all' -- all about a fungus. So how can we ever incorporate 'all' in our system?

KENDRICK: That is part of Dr. de Hoog's message (Chap. 14). He says that because you can never know the criteria by which nature orders itself, you can never claim to have constructed a natural classification. So now we've had three definitions. 'Natural' meaning based on the teleomorph only; 'natural' meaning based on teleomorph plus anamorph(s) -- all *available* information; and 'natural' meaning based on all *possible* information. This is surely, like the holomorph, an idealized concept that is intellectually stimulating, but we must not worry if we can't produce it by the day after tomorrow. We can only aspire to a more nearly natural system.

CARMICHAEL: Not me. I think that for anamorphs we have a special purpose classification based on morphology. It is highly useful for identification, and it is what we need.

LUTTRELL: It may be based on morphology now, but I believe it will be more broadly based in the future, as data accumulate.

CARMICHAEL: I'm talking about the classification of the anamorphs, not about the classification of the fungi.

LUTTRELL: The anamorph may *be* the fungus. I personally don't believe that, but many people do think that a large number of fungi exist only as anamorphs.

CARMICHAEL: If and when you integrate these genera into the families and orders of Ascomycetes and Basidiomycetes, you are integrating them into the general purpose classification. When you put them into a separate group -- an additional classification of the same species -- it has to be a special purpose classification. In the Zygomycetes we have a single classification. Whether we find the zygospores or not, they go into the same genus. But in the Ascomycetes and Basidiomycetes they *don't* go in the same classification. If you don't find the teleomorph you are forced to put them into a different, special purpose classification founded on 'form' (anatomical) taxa. Form genera have nothing to do with phylogeny, and Mr. Mason (1937) suggested that the loss to practical mycology would be negligible.

KENDRICK: Dr. Madelin has asked a good question: 'How do we know when we have a holomorph?' If we have one teleomorph and one anamorph, how do we know there isn't another anamorph -- or more than one -- lurking in the undergrowth? We don't. So when do we speak of holomorph?

HENNEBERT: The holomorph is all known and all unknown states of the fungus: the whole fungus, in all its manifestations, some of which we may not know. But once we have attached a holomorphic name to the part we know (the Botanical Code insists that this name must be applied only if we have the teleomorph) that name will cover all future discoveries.

MÜLLER: But this means there are actually three kinds of holomorph: (1) a teleomorph without any anamorph; (2) a teleomorph with one or more anamorphs; (3) an anamorph or anamorphs with no teleomorph. We could treat this last case as a holomorph unless and until we find that there actually is a teleomorph.

HENNEBERT: Yes, but for the present, the Code does not recognize the names of anamorphs as holomorphic names.

And as the discussion gravitated, seemingly inevitably, toward nomenclature once more, we decided that it was time to move from theoretical considerations to the very practical question of how a holomorphic fungus can be persuaded to exhibit its full range of somatic potential, and if there are any magic formulae which will enable us to produce anamorph(s) and teleomorph at will. As Dr. Müller relates, the picture which emerges from physiological studies is confusing and often contradictory, clearly springing from the diverse ecological requirements evolved by the fungi as they settled into their multitudinous niches.....

16
Factors Inducing Asexual and Sexual Sporulation in Fungi (mainly Ascomycetes)

E. Müller

INTRODUCTION

The fructification is the most conspicuous of all fungal manifestations, ensuring both survival and dispersal. Because these fructifications are so diverse while their individual characteristics are so stable within taxa, they provide the main data base for the existing taxonomic arrangement of the fungi.

Fungi fruit in two principal -- and quite different -- ways. The asexual fructification (the anamorph), which requires no change of nuclear phase, serves for quick propagation; whereas the sexual fructification (the teleomorph) typically involves a nuclear phase change which facilitates exchange of genetic information in addition to propagation.

Sometimes the kind of fructification formed under natural conditions appears to be determined entirely by the season. In pure culture under laboratory conditions, however, fruiting is often irregular or absent. It is often easier to obtain asexual than sexual fructifications: this shows that environmental factors may be decisive.

The problem of determining which conditions are favourable for fungal fructification is not new. The rules given by Klebs (1898, 1899, 1900), one of the first to concern himself with this matter, can be expressed as follows:

- sporulation occurs readily when a well-nourished thallus either exhausts its food substrate, or is transferred to a depauperate substrate.
- the range of nutrient concentration that will support vegetative growth is wider than that which will permit fructification.

But these rules are too general. Basing his conclusions on much better information, Cochrane (1958) pinpointed the vital factors as carbohydrate and nitrogen nutrition. He also considered other growth factors, and recognized the importance of some physical factors. More recent reviews of fungal reproduction (Machlis 1966, Hawker 1966) differed from Cochrane only in detail. Others (Cantino 1966, Turian 1966, 1969, Taber 1966) discussed morphogenesis as a whole, and considered reproduction as just one stage in the life cycle.

Since I cannot review the entire literature on fructification, I refer the reader to the fundamental papers just mentioned. The examples on which I base my discussion are drawn from the Ascomycetes and Deuteromycetes.

Neither anamorphs nor teleomorphs develop in a smooth, continuous process, but rather in a series of steps, some of which may require different environmental conditions. Experimental

work on *Neurospora africana* Huang & Backus shows that at least four different steps may be involved in the development of ascomata: development of protoperithecia; differentiation of ostiolate perithecia; development of asci; differentiation of ascospores. Each of these steps may be triggered by a single amino acid, as shown in Table 16.1.

Table 16.1. Influence of nutrition with some single amino acids on the development steps of *Neurospora africana* teleomorph. Amino-acids in L-form added to substrate with glucose and mineral salts.

Nitrogen source	Development of: Protoperithecia	Perithecia	Asci	Ascospores
Methionine	-	-	-	-
Tryptophane	+	-	-	-
Alanine	+	+	-	-
Phenylalanine	+	+	+	-
Isoleucine	+	+	+	+

+ development step induced
- development step not induced

ENDOGENOUS FACTORS

Genetic factors decide not merely the ability or otherwise of fungi to fruit, but their myriad reactions to environmental influences. Many fungi exhibit both asexual and sexual fructifications, but the majority appears to lack one or other of these, and we are far from knowing all possible fructifications of all fungi. This Conference charts both our knowledge and our ignorance in this area.

While some fungi may never produce a particular kind of fructification, others, initially possessing that ability, may lose it. It is well known that long-term culturing under laboratory conditions may depress or even suppress the fruiting of many fungi. Some remedial measures are also well-known: ringing the changes in substrate; using fruiting structures rather than sterile mycelium as inoculum when transferring cultures; using a natural substrate (e.g., plant parts, cereal grains) instead of artificial or defined media. And, fortunately, we know many fungi that fruit rapidly and profusely on ordinary laboratory media, even after innumerable transfers.

Sexual processes depend on the propinquity of sexually different but compatible nuclei ready to fuse. In many cases these develop within morphologically distinct cells (gametangia) which may be discerned with varying degrees of difficulty. But the majority of Ascomycetes and most Basidiomycetes do not produce morphologically differentiated gametangia, and the presence of compatible nuclei can be confirmed only by the discovery that sexual processes are under way.

Most fungi are monoecious, with male and female (or + and -) nuclei both present within a thallus originating from a single spore. Dioecious fungi with sexually different thalli

arising from single spores are uncommon (e.g., *Achyla* species). In such cases, sexual fructification can only happen when sexually different thalli meet (Esser & Kuenen 1967). A similar complication occurs within 'Heterothallic' (i.e., self-incompatible) monoecious fungi. The male and female gametangial cells of any given monosporic thallus are presented from fusing by built-in incompatibility factors, and sexual fusion is possible only between thalli with different incompatibility factors. Bipolar incompatibility (involving two incompatibility alleles) is characteristic of Ascomycetes; bipolar or tetrapolar incompatibility (the latter involving four incompatibility alleles) are characteristic of Basidiomycetes (for details, see Esser 1966, Raper & Flexer 1971). An example of bipolar incompatibility is shown in Plate 16.1a,b.

The development of ascomata arranged in distinct concentric rings may be induced by the diurnal rhythm of light and darkness (Hawker 1966). The same phenomenon may also appear without any change in light or, for that matter, any other environmental factor. This is seen in cultures of *Chaetomium uniporum* Aue & Müller. The rhythmic development of the fungus seems to be genetically fixed (Plate 16.1c).

ENVIRONMENTAL FACTORS

Fungi will fruit only if climatic and edaphic factors are appropriate. In our experience, none of these factors acts independently. Sporulation is stimulated only if the sum of influences is favourable. Another complication is that any given factor may sometimes favour and at other times depress fructification, depending on the behaviour of the species concerned or on the presence or absence of other influences: controlled experiments can be very difficult to devise. Investigations of the effects of environmental factors are thus extremely complicated, and experimental results must be interpreted with caution. The value of all information is relative, and results apply only to the specific conditions and the specific organism tested. Despite these difficulties, the effects of single environmental factors must be considered.

CLIMATIC FACTORS

TEMPERATURE strongly influences both vegetative growth and fruiting of fungi. Fructifications usually develop over a narrower range of temperature than that which permits vegetative growth. Sexual and asexual fructifications may have different temperature requirements, the range for sexual reproduction often being narrower than for asexual sporulation. In many cases, sexual reproduction is favoured by comparatively low temperatures.

The mesophilic *Talaromyces helicus* var. *helicus* (Stolk & Samson 1972) will grow at 40°C, but conidia are not produced above 37°C, and sexual reproduction is inhibited above 32°C. The thermophilic *Talaromyces emersonii* Stolk, which will grow between 30°C and 55°C, fruits asexually from 35-54°C, but sexually only from 31-47°C (Müller 1973). Note, however, that *Ceratocystis fimbriata* Ell. & Halst. produces conidia best at 18°C, ascomata at 25°C (Barnett & Lilly 1947).

Temperature change may induce minor or even major alterations in the morphology of fructifications. Luttrell (1963) reported for *Cochliobolus sativus* (Ito & Kurib.) Drechsl. (sub *Helminthosporium sorokinianum* Sacc.), that proliferation of the conidiophore, though normal-

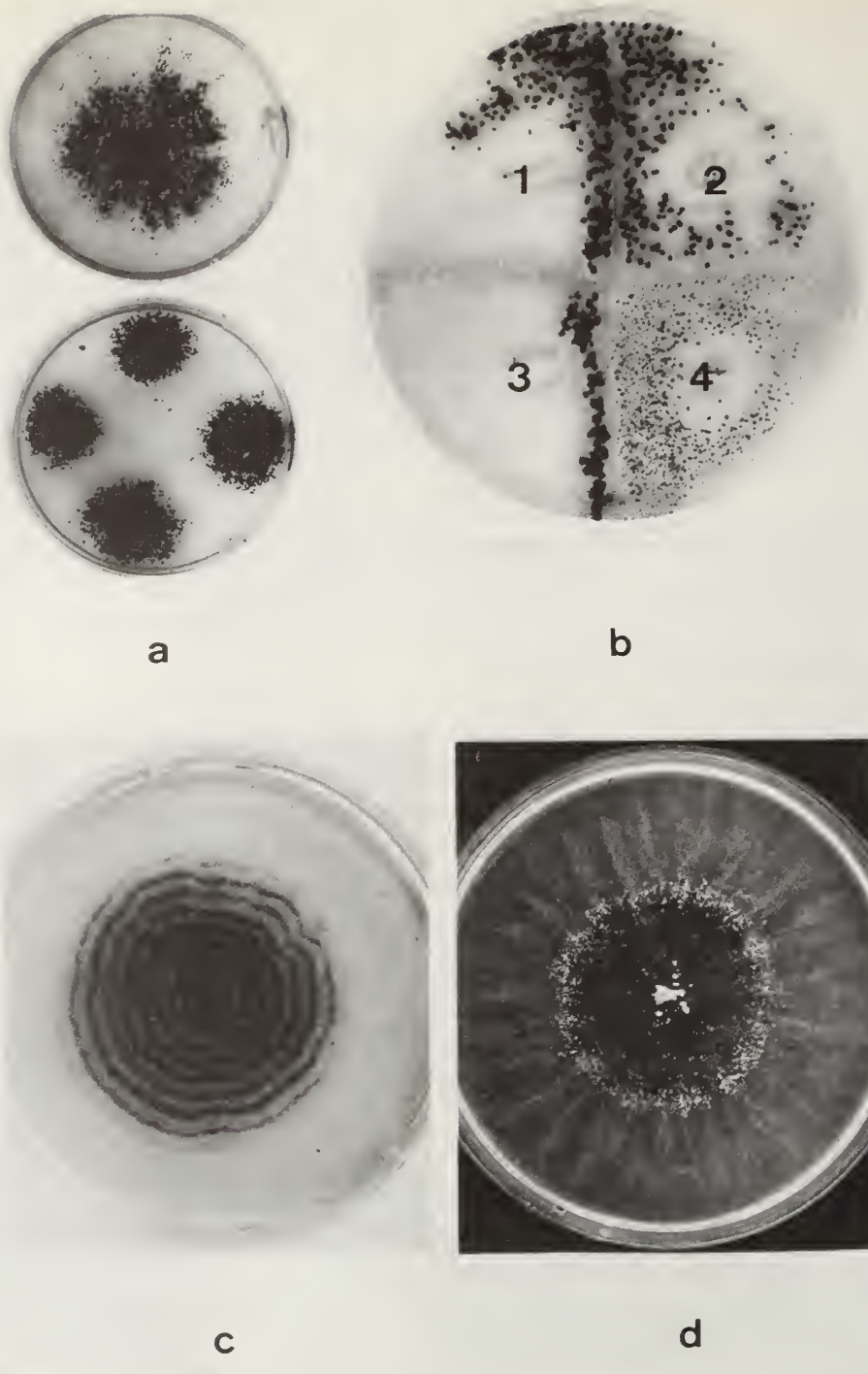


Plate 16.1 A, *Chaetomium elatum* Kunze & Schm. ex Fr., fructification of monascosporic, homothallic (=self-compatible) strains. B, *Chaetomium elatum*, fructification behaviour of four monascosporic heterothallic (=self-incompatible) strains. Strains 1 and 3, 2 and 4 respectively have corresponding incompatibility factors, fructification is therefore not possible between 1 and 3 or 2 and 4. Normal fertilization takes place in the combination 1 and 2, whereas in the combination 3 and 4 normal fertilization is only possible from 4 to 3 but not from 3 to 4. C, *Chaetomium uniporum* Aue & Müller, genetically determined growth rings with fructifications. D, *Trichoderma pseudokoningii* Rifai, light-induced growth ring with conidial fructification.

ly lateral (i.e., sympodial) became percurrent at high temperatures. In *Drepanopeziza ribis* (Kleb.) Höhn. (Blodgett 1936) and *Gnomonia leptostyla* (Fr.) Ces. & de Not. (Fayret 1975), low temperatures favour not only the development of young ascomata, but also the occurrence of 'microconidia' which may be spermatia. As temperature increases, macroconidia tend to be produced in place of microconidia.

The induction and the maturation of ascomata in *Pleospora herbarum* Rabenh. require different temperatures (Leach 1970). The induction of protoperithecia in *Neurospora crassa* Shear & Dodge, and their subsequent maturation, depend on the temperatures prevailing before and after fertilization occurs (Hirsch 1954).

LIGHT. The influence of light on fructification is more complex. A number of workers have reported that their experimental organisms fruit equally well in light and in darkness, e.g., some strains of *Leptosphaerulina* (Graham & Luttrell 1961, Müller 1966, Leach 1971, Leach 1972), and *Talaromyces emersonii* (Müller 1971). Even in such cases, light may sometimes influence the size and shape of spores or spore-bearing structures, as in *Sordaria fimicola* Ces. & de Not., which produces longer ascospores in cultures exposed to light (Hawker 1966). The zygomycetous *Thamnidium elegans* Link produces both sporangioles and multispored columellate terminal sporangia in the light: in darkness only sporangioles are formed (Lythgoe 1961).

In other cases the influence of light on reproduction is obvious. Sometimes there is an absolute requirement for visible and non-visible light, but radiation may also depress or even suppress reproduction. Asexual and sexual states of the same fungus often respond differently to radiation. It has been repeatedly demonstrated that the near-UV and long-wavelength UV have the greatest influence on fructification. As shown in Tables 16.2 and 16.5, the effects of light may be modified by those of other factors such as temperature or nutrition. We must therefore interpret many statements on the light-induction of sporulation with caution, because they are not accompanied by precise descriptions of other relevant conditions.

Fructification of *Pleospora herbarum* is induced by near-UV wavelengths from 237-366 nm (Leach 1963). This applies both to the ascomata and the *Stemphylium* anamorph. A few ascomata may also form in the longer-wavelength violet light, but they will not mature in this light. The *Stemphylium* state sporulates in two stages: conidiophore development requires radiation, while conidia form only in darkness, and their maturation is inhibited by radiation. The ascomata also mature only in darkness, which should be combined with low temperature (Leach 1968, 1971). In *Talaromyces helicus* (Raper & Fennell) C.R. Benj. production of conidia is favoured by near-UV as well as by violet and blue light, while development of ascomata is distinctly depressed by such conditions, being favoured by darkness, red or yellow light. As shown in Table 16.5, nutritional factors may modify light-responses. A similar reaction has been reported for *Gnomonia leptostyla* by Fayret (1975). The sporulation of *Botrytis cinerea* Pers. is potentiated by near-UV light. A complicated interaction of near-UV, blue, red, and far-red light was demonstrated by Tan (1974a,b,c, 1975a,b) and Tan & Epton (1973, 1974). The potentiation by near-UV can be reduced by treatment with blue light. Subsequent exposure to near-UV restores sporulation to the potential level, and this can again be nullified by further doses of blue light. Periods of darkness interposed before the later

treatment with blue light reduce the effectiveness of the blue light. Far-red light stimulates sporulation much in the manner of near-UV, and this effect of far-red is reversible by exposure to red or blue light.

The duration of light-stimulation necessary to induce fruiting varies widely. Non-sporulating cultures of *Trichoderma pseudokoningii* Rifai, transferred and incubated in darkness, were exposed to daylight for a few seconds, then kept in the dark once more. After one day, a peripheral ring of sporulation appeared. Longer exposures to the light induced wider zones of sporulation. We may conclude that, at least in this case, the hyphal tips are most sensitive to light-stimulation (Plate 16.1d).

In contrast to the above, cultures of *Gnomonia leptostyla* require a long, uninterrupted exposure to light for the best induction of fruiting, as shown in Table 16.2. There is also a considerable difference in sporulation in continuous light as compared to a regime of alternating 12-hour periods of light and darkness.

In some cases the effects of temperature and light are interconnected. Table 16.2 shows the mutual dependence of these factors in *Gnomonia leptostyla* (Fayret 1975). Low temperature permits development of ascomata in the light, whereas higher temperatures plus light depress the formation of ascomata. In contrast, asexual reproduction is inhibited by darkness combined with low temperature, while higher temperature appears to be more favourable to the formation of conidia.

WATER supply may be an important factor in certain groups of fungi. Wilson (1928) demonstrated that *Venturia inaequalis* (Cke.) Wint. needs high humidity, not only for initiation of ascomata in autumn, but also for their maturation in spring. Similar observations have been made by von Arx (1957) on cultures of *Venturia chlorospora* (Ces.) Karst. on *Salix* leaves. In high humidity this fungus precociously completed the development of its ascomata during the autumn. These observations have been confirmed by Nuesch (1960).

The seasonal differences found in fungal fruiting may be imposed by the characteristic seasonal regimes of temperature and light, especially in temperate or cold climates, which have sharp differences between summer and winter. The ascomata of many Ascomycetes mature during spring or early summer, indicating that their development begins in winter. In contrast, many anamorphs develop during the summer. This kind of developmental rhythm is well known in many plant-pathogenic Ascomycetes, such as *Venturia* species (anamorphs *Fusicladium, Spilocaea, Cladosporium, Pollaccia), Pyrenophora* species *(Drechslera),* and *Gnomonia* species *(Cylindrosporella, Discula).*

Leach (1971) found for *Pleospora herbarum* that development of ascomata was induced not only by UV, but also by long periods of darkness at low temperature. Maturation of the ascomata always required long, uninterrupted periods of low temperature, light apparently being unnecessary. While asexual reproduction is favoured by a diurnal regime of fluctuating temperatures and alternating light and darkness (Leach 1968), sexual fructification is much less affected by such daily changes. It is apparent that the development of sexual fructifications is adapted to winter conditions with long periods of low temperatures, perhaps under snow cover, whereas asexual reproduction is best suited to summer conditions. The development of the ascomata of some *Venturia* species may also be explained by their adaptation to winter conditions of low temperature, low light (especially under the snow) and sporadic high

Table 16.2. Influence of temperature and light conditions on asexual and sexual fructifications of *Gnomonia leptostyla* (Fayret 1975).

Temperature °C	Fructification					
	asexual			sexual		
	Continuous Darkness	12 hours Darkness 12 hours Light	Continuous Light	Continuous Darkness	12 hours Darkness 12 hours Light	Continuous Light
7	0	0	+[1)]	+++	+++	++
10	0	+	++[1)]	+++	+++	++
14	0	++	+++[2)]	++++	++	+
18	0	+++	++++[2)]	++++	+	rare
21	rare	++++	++++[3)]	++	rare	0
25	++	+++	+++[3)]	±	0	0

0 = no fructification

\+ = fructification possible, number of crosses indicates the relative number of fructifications.

1) = mainly microconidia (spermatia)

2) = microconidia and macroconidia in equal numbers

3) = mainly macroconidia.

Table 16.3. Influence of different carbon sources on the development of fructification in different Ascomycetes (Bolay 1971, Fayret 1975, Müller 1966).

Carbon source	Fruiting reaction of:					
	Gnomonia comari		*Gnomonia leptostyla*			*Leptosphaerulina australis*
				sexual		only sexual
	asexual	sexual	asexual	Protoperithecia	mature	
Na-acetate	0	0	+	0	0	0
L-Arabinose	+	0	0	0	0	+
L-Rhamnose	0	0	0	0	0	0
D-Xylose	+	0	0	0	0	+
D-Fructose	+	0	+	+	+	+
D-Galactose	0	0	0	0	0	+
D-Glucose	+	0	+	+	+	+
D-Mannose	+	0	0	0	0	+
L-Sorbose	0	0	0	0	0	0
D-Cellobiose	+	0	+	+	+	+
Lactose	0	0	+	+	0	+
Maltose	+	0	+	+	(+)	+
Sucrose	+	+	+	+	+	+
D-Trehalose	+	0	+	+	+	-
Raffinose	+	+	+	+	+	+
Dextrin	+	0	+	+	(+)	+

\+ fructification possible, 0 fructification not possible - no results

humidity. The observation that similar temperatures are required by the fungus for the development of mature ascomata and by the host for the development of its leaves, has been made by Borecki (1957) for *Venturia pirina* Aderh. on *Pirus communis* and by Stojanovic (1958) for *Venturia inaequalis* on *Pirus malus*.

EDAPHIC FACTORS

pH. Little attention has been paid to the influence of environmental pH on fungal fructification. Experimental work of this kind is difficult because any change in pH changes other factors just as important for sporulation as the one being tested. Thus, interpretation of results from such experiments must include considerations of these other factors. Even the experimental design must be scrutinized to make sure that pH is actually the factor being tested.

Judging from the few such experiments that have been done, we can conclude that the range of pH favouring fruiting is narrower than that permitting vegetative growth. *Leptosphaerulina australis* McAlp. will grow within the range pH 3-10, but will fruit only from pH 4-9 (Müller 1966). Narrower ranges were reported by Lockwood (1937) for *Chaetomium* sp., *Eurotium herbariorum* (Pers.) Link ex Fr., and *Eupenicillium javanicum* (van Beyma) Stolk & Scott. Recent experiments with *Monascus ruber* van Tieghem have shown that while vegetative growth is possible between pH 2.3 and 7.4, formation of the teleomorph and anamorph is favoured by the lower pH values, but their development is depressed above pH 6.5.

OSMOTIC PRESSURE. Some ascomycetous and deuteromycetous fungi colonizing substrates such as cereals, fruit juices, or salty foods, are adapted to, or even require, an environment with high osmotic pressure. *Eurotium* species are the best-known osmophilic fungi (Curran 1971, Blaser 1976), but *Byssochlamys* species may share this predilection (Beuchat & Toledo 1977). Most *Eurotium* species grown and fruit asexually at a water capacity (a_w) of 0.86, though sexual fructification is inhibited in most species except *E. amstelodami* deBary. Some *Eurotium* species, for example members of the *E. echinulatum* group, cannot grow in media with low osmotic pressures (a_w = 0.99 - 1.00), but *E. amstelodami* demonstrates its versatility by fruiting even at such low osmotic pressures.

NUTRITION. This seems to be the most complex of all edaphic factors influencing fungal fructification. Experimentation in this area is difficult both to plan and to interpret. It is almost impossible to change one nutrient without disturbing others. The food substances made available may be absorbed directly, or they may be broken down into smaller, more easily assimilable units. the type and amount of nutrients, and their interactions, decide the manner and rate of their uptake. The reduction in concentration of one nutrient concomitant upon its uptake by the fungus may alter the uptake of other nutrients. All these factors must be considered in the planning and execution of the experiments. Despite these difficulties, certain trends can be recognized.

It is widely accepted that sexual reproduction often depends on the carbon-nitrogen balance in the medium (Turian 1966, Müller 1966). In addition to this quantitative effect, there are other effects caused by qualitative differences in the various basic nutrients. Among carbohydrates, sugars often favour fructification, although they differ widely in their effects. Table 16.3 summarizes the results of experiments with *Gnomonia comari* Karst. (Bolay

1971), *Gnomonia leptostyla* (Fayret 1975) and *Leptosphaerulina australis* (Müller 1966). Sorbose and rhamnose did not permit any fruiting, while at the other end of the scale raffinose and saccharose induced both asexual and sexual fructifications in every case. The other sugars fell between these two extremes in their effects on fructification. It is of interest to note that more sugars favour asexual than sexual reproduction. Polysaccharides may also promote fruiting.

The effects of nitrogen source on fruiting (Table 16.4) vary so profoundly from one source to the next, and from one species to another, that it seems impossible to draw any general conclusions about the four experimental organisms concerned: *Gnomonia comari* (Bolay 1971), *Gnomonia leptostyla* (Fayret 1975), *Neurospora africana* and *Talaromyces helicus*. As Table 16.1 shows, the effects of different amino acids on the successive steps of ascoma development in *Neurospora africana* may be entirely different.

The effects of the various nitrogen sources are also influenced by other factors such as light and temperature, as shown in Table 16.5, which summarizes experiments with *Talaromyces helicus* and *Talaromyces emersonii*. Fayret (1975) observed similar phenomena in *Gnomonia leptostyla*. Although these interactions have been clearly demonstrated, the reasons for such divergent reactions to the various nitrogen sources remain obscure. The different responses to D- and L-forms of alanine and serine, or to aspartic acid and asparagine, or glutamic acid and glutamine, are especially puzzling. Even some of the simplest nitrogen sources, such as nitrate or ammonium, do not elicit uniform responses. While ammonium compounds promote sexual reproduction better in *Talaromyces helicus* (Müller 1971) and *Gnomonia leptostyla* (Fayret 1975), nitrate is superior in this respect in *Talaromyces emersonii* (Müller 1971), *Leptosphaerulina australis* (Müller 1966) and *Gnomonia comari* (Bolay 1971).

Fungi also react differently to the C:N ratio found in their substrate. Figure 16.1 shows two examples. *Talaromyces helicus* fruits sexually when the C:N ratio is between 10:1 and 240:1 as long as total C does not exceed 33 g/l (Müller 1971). This means that for fructification a high carbon level must be accompanied by a relatively high nitrogen level. Lower carbon levels will only promote fruiting if the nitrogen level is also reduced. *Leptosphaerulina australis* has exactly the opposite requirements (Müller 1966). When carbon concentrations are high the fungus will fruit only if the nitrogen level is correspondingly low. In high nitrogen concentrations, fruiting requires low carbon levels. The effect is more distinct with ammonium nitrogen than with nitrate. Similar responses have been reported for *Neurospora crassa* by Westergaard & Mitchell (1947).

Hall (1971) showed that production of perithecia in *Sordaria fimicola* (Rob.) Ces. & de Not. was best at C:N ratios of 5:1 or 10:1 when C is present as glucose or maltose, and N as potassium nitrate. A direct comparison with *Talaromyces helicus* and *Leptosphaerulina australis* is difficult because the nutrient concentrations for *Sordaria* were relatively low. We may suggest that *S. fimicola* behaves like *Leptosphaerulina*.

Convincing reports on the influence of other nutrients on sporulation are comparatively few. However, there is no clear evidence for a qualitative difference between requirements for vegetative growth and reproduction. Only calcium may represent an exception. Its stimulating effect on fruiting in *Chaetomium globosum* Kunze ex Fr. was demonstrated by Basu (1951), though it has no influence on vegetative growth. Papers on mineral nutrition re-

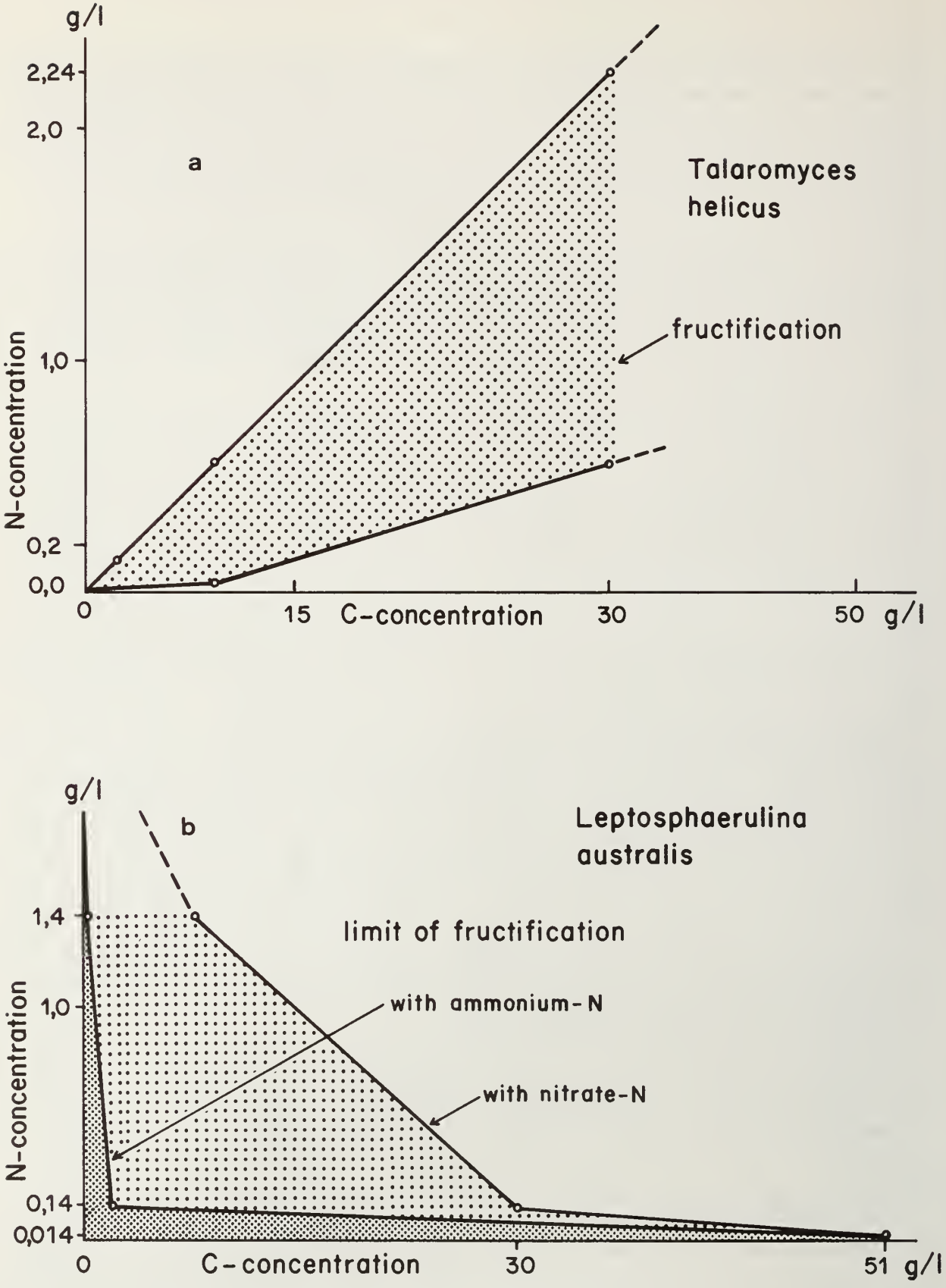


Fig. 16.1 Reactions of *Talaromyces helicus* and *Leptosphaerulina australis* to changes in relative concentrations of C and N.

Table 16.4. The influence of different N-sources on the fructification of various Ascomycetes, (information partly based on Bolay, 1971 and Fayret, 1975).

N-sources	Fruiting reaction of								
	Neurospora africana	*Gnomonia comari*		*Gnomonia leptostyla*		*Talaromyces helicus*		*Talaromyces emersonii*	
	sexual	asexual	sexual	asexual	sexual	asexual	sexual	asexual	sexual
$-NO_3$	0	+	+	0	0	+	+	0	+
$(NH_4)-$	0	+	0	+	+	+	+	+	+
Glycine	0	+	0	-	-	+	0	+	+
Alanine	0	+	0	+	+	+	+	+	+
Valine	+	0	0	+	0	+	+	+	+
Leucine	0	0	0	+	0	+	0	+	+
Phenylalanine	0	+	0	0	0	0	+	+	+
Proline	0	+	0	0	+	+	0	+	+
Serine	0	+	0	+	+	+	0	+	+
Threonine	+	+	0	0	0	+	+	+	+
Tryptophane	0	0	0	0	0	+	+	+	0
Tyrosine	0	+	0	-	-	+	0	+	+
Methionine	0	+	0	-	-	+	+	+	+
Asparagine	0	+	0	0	0	+	+	+	+
Aspartic acid	0	+	0	+	+	+	0	+	+
Glutamine	+	0	0	0	0	+	0	+	+
Glutamic acid	0	+	0	+	+	+	+	+	+
Arginine	+	+	0	+	+	+	+	+	+
Histidine	0	+	0	-	-	+	+	+	+

+ fructification possible, 0 not possible. Amino acids in mixed D- and L-forms or only in L-form. Results of *Gnomonia* and *Talaromyces* species from exposed or unexposed cultures or broth.

Table 16.5. The influence of different nitrogen sources on the fructification of two *Talaromyces* species.

N-sources	*Talaromyces helicus*				*Talaromyces emersonii*			
	asexual		sexual		asexual		sexual	
	dark	light	dark	light	37°C	45°C	37°C	45°C
KNO_3	0	+	+	0	+	+	+	+
$(NH_4)_2HPO_4$	0	+	+	0	0	0	+	+
$(NH_4)_2SO_4$	0	+	+	0	+	+	+	+
L-Alanine	+	+	0	0	+	+	+	+
D-Alanine	+	+	+	+	+	+	+	0
L-Serine	+	+	0	0	+	+	+	+
D-Serine	+	+	+	+	+	0	+	0
Aspartic acid	+	+	0	0	+	+	+	0
L-Asparagine	+	+	+	+	+	+	+	0
Glutamic acid	+	+	+	+	+	+	+	+
L-Glutamine	+	+	0	0	+	+	+	+
L-Cystine	0	+	+	+	+	0	+	0
L-Tyrosine	+	+	0	0	0	+	+	+
L-Tryptophane	+	+	+	+	+	0	0	0
L-Ornithine	0	+	+	+	0	0	+	0
L-Arginine	+	+	+	+	0	+	+	+

+ fructification possible 0 not possible

viewed by Forster (1939) do not prove that such nutrients are the sole or the principal agents in the induction of sporulation (Cochrane 1958). According to Buston et al. (1954), Buston & Rickard (1956), and Basu (1951), phosphate and calcium have some stimulatory effect on fruiting in *Chaetomium* species.

Müller (1971) reported that phosphate depressed fructification in *Talaromyces emersonii*. In a comparison between ammonium sulphate and ammonium phosphate, the latter in higher concentrations depressed growth and sexual reproduction, and inhibited the formation of conidia.

Sporulation of *Aspergillus niger* van Tieghem, *Phoma betae* Frank, and *Penicillium* species may be drastically reduced by copper deficiency (Metz 1930, Mulder 1939, Steinberg 1935, 1936) though this had little or no effect on vegetative growth. The same phenomenon results from partial deficiencies of other heavy metals (Cochrane 1938).

Auxotrophic fungi such as *Sordaria fimicola* often need more biotin or thiamine for reproduction than for vegetative growth (Barnett & Lilly 1947). *Sordaria macrospora* Auersw. requires biotin in order to produce perithecia, and the number of perithecia which develops is a function of the biotin concentration (Molowitz et al. 1976). *Ceratocystis fimbriata* requires thiamine in proportion to the total nutrient concentration of the medium (Lilly & Barnett 1947).

The results of experimental work on the influence of environmental factors on reproduction may suggest optimal formulations of media for growth and the complete differentiation of all reproductive structures. Fayret (1975) has proposed such a medium for *Gnomonia leptostyla*. In addition to a number of mineral compounds, it contains 5 g/l glucose, and either aspartic acid or a mixture of alanine and serine in concentrations equivalent to 50 mg N/l.

INDUCER SUBSTANCES AND METABOLIC PATHWAYS

Unfortunately, the connection between environmental factors and the occurrence or repression of reproduction has been only partially explored. The literature on substances responsible for the development of fruiting structures (e.g., sex hormones) has been reviewed by Machlis (1966). Little is known about the chemistry of such substances, and only a few examples are known in which environmental factors might be involved in their occurrence.

Leach (1965) isolated from sporulating cultures of *Ascochyta pisi* Lib. a substance provisionally named 'P 310' (maximum absorption in the region of 310 nm wavelength). This substance is present in cultures exposed to UV, but also in cultures grown on media which support sporulation in the absence of inducing radiation. P 310 is absent from non-sporulating colonies. If it is added to such cultures incubated in the dark, sporulation begins. P 310 does not seem to be specific, because a number of other Deuteromycetes, Ascomycetes and even Basidiomycetes were also stimulated to produce reproductive structures (Leach & Trione 1965, Trione et al. 1966). P 310 may be related to a photoreceptor, but its apparent absence in non-sporulating cultures in the dark, and its presence in some cultures sporulating in the darkness, seems to contradict the photoreceptor hypothesis. In recent papers on photo-absorbing substances isolated from different Ascomycetes and Basidiomycetes, Favre-Bonvin et al (1976) and Arpin et al. (1977) reported on several compounds absorbing at 310 nm, which seem to be identical with P 310. These "mycosporines" are cyclohexonones linked with amino acids, e.g., serine, reduced serine and cyclic glutaminic acid. It is suggested that they have an

active role in amino acid transport. According to Surapipith & Lindemayer (1969) flavines may represent photosensitive compounds in *Sordaria fimicola*.

Much work has been done with the self-incompatible *Neurospora* species. Looking for a better defined crossing medium, Westergaard & Mitchell (1947) observed that *Neurospora crassa* grown on an optimal medium failed to produce perithecia at 35°C. Hirsch (1954) demonstrated that tyrosinase and melanin are reduced or absent in such sterile mycelia. He further showed that any condition inhibiting melanin production also inhibited the formation of protoperithecia. However, a direct connection between melanin production and formation of protoperithecia could not be confirmed experimentally. According to our own experiments with the self-compatible *Neurospora africana*, melanin was absent but perithecia were produced on a medium containing ornithine as the sole nitrogen source. The direct induction of protoperithecia by melanin seems questionable.

Turian (1960, 1961a,b, summarized 1966, 1969) demonstrated a strict connection between conidium formation and a lesion in the Krebs cycle of *Neurospora* species, while morphogenesis of protoperithecia apparently required full functioning of this metabolic pathway. Inhibition of the Krebs cycle and induction of the glyoxylic acid cycle by acetate nutrition strongly repressed protoperithecial differentiation and favoured asexual reproduction. A similar reaction was demonstrated by Fayret (1975) for *Gnomonia leptostyla*.

DISCUSSION

At present we cannot properly survey the connections between factors potentially influencing reproduction and their actual effects on the fruiting behaviour of fungi. The fragmentary information presented in the preceding pages does not allow any precise generalization, although some effects persist across several examples. As long as we do not know the complex metabolic pathways involved in the induction and in the development of fructifications, only preliminary suggestions about these events seem to be possible.

On the other hand we can suggest some general rules on the action of these factors:

1. Under given conditions fertility or sterility of growing fungal colonies results from the *sum* of external (environmental) and internal (genetic) influences, as has been demonstrated in *Gnomonia leptostyla* (Table 16.2) (Fayret 1975) and *Talaromyces helicus* (Müller 1971).
2. The effect of any environmental factor may often be replaced or duplicated by the effect of other factors. For example, light influence by special wavelengths can be replaced by nutrition with certain amino acids in *Talaromyces helicus* (Table 16.5).
3. Any environmental factor influencing fungal fructification may function as a promotor or as an inhibitor. For example, light favours asexual fructification and inhibits sexual fructification of *Talaromyces helicus* and *Gnomonia leptostyla;* phosphate favours sexual fructification in *Chaetomium* and depresses sexual and asexual fructification in *Talaromyces emersonii*. The kind of influence depends on the fungal species, on the kind of reproduction (sexual or asexual), and on other influences acting under given conditions.

ACKNOWLEDGMENTS

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DIALOGUE FOLLOWING DR. MÜLLER'S PAPER

Temperature

LUTTRELL: I have a specific question about a species of *Gnomonia*. How high a temperature is needed to induce the anamorph? Even at 27°C I had a preponderance of perithecia over pycnidia.

MÜLLER: Usually the range for the anamorph is wider than for the teleomorph, and the teleomorph is favoured by the lower end of the range. This is a general rule, though some fungi exhibit exactly the opposite behaviour. You have an exception to the rule.

VON ARX: The Mucorales produce sporangia under a very wide range of conditions, but the zygospores are often formed only on special media, only within a narrow range of temperatures, only in the light (or sometimes only in darkness). So narrow are some of these ranges that we can use them to key out species: 'producing zygospores at 16°C' or 'producing zygospores at 20-25°C'.

BENJAMIN: *Thamnidium elegans* produces zygospores only in very cold conditions -- 4-6°C.

KENDRICK: Does anyone else have experiences of this kind, concerning the induction of fruiting, that he or she would like to share with us?

WATLING: In the Basidiomycetes I have found it very useful to capitalize on one's field knowledge. In Britain *Armillaria mellea* usually fruits after the first frost or when there has been a sharp drop in temperature. Most people have had great difficulty getting *Armillaria mellea* to fruit in culture, but if one lowers the temperature to 5°C overnight, this will consistently induce fruiting. *Conocybe* species fruit best in cultures with a very high pH. This is a logical deduction from the observation that they normally occur in nature on base-rich soils.

MADELIN: I suspect that most of us grow fungi at too high a temperature anyway. Some years ago one of my students found that *Cordyceps militaris* fruited well at 18°C, but not at 23°C or above. Cooler conditions may often make a real difference.

BENJAMIN: I routinely grow some species of *Piptocephalis* at 18°C, because at 25°C they will not survive many transfers. I believe Dr. Schipper has found that the mating types of some heterothallic Mucorales lose their sexual vigour when kept at room temperature, but regain it after prolonged cold treatment. I'm going to try this on some *Helicostylum* and Thamnidiaceae isolates that appear to have lost their ability to produce zygospores.

MADELIN: The area between 5 and 10°C is an important one whose effects have not yet been adequately explored. Ogunsanya & Madelin (1977) have recently found that cooling some spores below 10°C renders them lethally sensitive to being wetted. This is a temperature range that occurs often in nature, and needs a closer look.

WERESUB: Many *Typhula* sclerotia will perform only within the temperature range of 4-10°C.

MADELIN: This is the kind of temperature at which phase changes occur in phospholipid membranes, which may be critical for permeability phenomena.

MÜLLER: In temperate and northern climates, the winter is often the decisive factor in fruiting patterns. Many species are adapted to developing their ascospores in cold and darkness, so that they will be ready to infect a host in early spring. We must remember that in laboratory experiments we cannot duplicate all the factors at work in nature.

LUTTRELL: Kurt Leonard (1976) discussed the initiation of fruiting in *Setosphaeria rostrata*. He gave the two mating types a long cold treatment prior to mating. After this they would mate and produce ascomata at ordinary temperatures. I found this amazing: if this discussion was not being recorded, I'd be tempted to say I found it incredible. This is in some ways comparable to the story in *Armillaria*.

WATLING: The need for a cold shock prior to fruiting was described by Denyer (1960) for *Pholiota alnicola* and *P. conissans*.

KENDRICK: We musn't forget such classical cases of cold requirements as the sclerotia of the Sclerotiniaceae, and the ergot of *Claviceps*, both of which need prolonged cold treatment -- at least six weeks -- before they will germinate.

WATLING: The *Armillaria* and *Pholiota* need to fruit immediately -- before the winter.

KENDRICK: And the others are designed to fruit *after* the winter. So the relative lengths of cold treatment required make sense. The agarics need a reminder to get on with the job before it's too late, the Ascomycetes are like seeds, and their dormancy mechanisms protect them from germinating too early -- for example during a warm spell in October or November.

WATLING: I agree with Dr. Madelin that we should pay more attention to the lower temperatures, especially as they occur in Nature. When I collected with Jack Warcup in November and December, looking for mycorrhizal fungi, we found many resupinate basidiomycetes which had not been considered before, yet Dr. Warcup was able to grow these fungi and synthesize mycorrhizae with them. We had missed them because we usually collected at other seasons: most mycologists go into hibernation at the end of October. But if you look during colder weather you'll find many species that have adapted to low temperatures.

KENDRICK: Fungi are often particularly good at growing in low temperatures. See how well they do at 4-7°C on some kinds of food in your refrigerator. And the amphibious Hyphomycetes do well at 0-4°C in streams during our Canadian winter.

WERESUB: I have collected beautifully sporulating basidiomata of resupinate fungi in January in Ottawa -- and that's frequently at well below freezing temperatures lasting several weeks. And I remember a culture of an Ascomycete (it may have been a *Pleospora*) that was stored in the ice compartment of a refrigerator: it fruited there and never again under any conditions.

KENDRICK: Even an agaric, *Flammulina velutipes*, fruits well in winter.

MALLOCH: So does *Cantharellula umbonata*. I have found basidiomata frozen solid -- but when you thaw them out they'll give a beautiful spore print. They obviously release spores whenever there's a mild spell.

KENDRICK: Does anyone have any observations on climates in which the conditions do not change substantially all year round?

LUTTRELL: The case of *Aulacostroma* is interesting (Luttrell & Muthappa 1974). The temperature in India was fairly uniform, though there was a monsoon -- a rainy season. The fungus turned out to have a normal annual cycle, just as you would find in Georgia or Ottawa. Infection occurred in 'Spring' -- after the dry season -- and ascoma development proceeded uniformly through the monsoon and was tuned so that it matured at the beginning of the dry season. It spent the dry season as a fully matured ascoma, but did not release its

spores until the spring rains, thus coinciding with the new growth of the host plants. Our temperate zone fungi differ only in developing very slowly throughout the adverse season -- ascospores maturing only in March or April.

MÜLLER: Some parasitic fungi are beautifully tuned to the development cycles of their hosts. The conditions necessary to induce apple and pear trees to produce young leaves are exactly those required to produce mature ascomata of *Venturia inaequalis* and *V. pirina*. When we investigate the fruiting of the teleomorph in particular, I think we should go back to the natural substrate, under natural conditions, and ask ourselves such questions as: When does the teleomorph occur? Where does it occur? What events lead up to fruiting? Only by careful observation in the field will we learn the secrets of many fungi. For example, although most fungi have an annual cycle, some take two years to complete their development. This is true of *Herpotrichia*, the snow mold of conifers.

LUTTRELL: This also happens in *Apiosporina (Dibotryon) morbosa*. In my experience infection takes place in early Spring, and the gall forms in Summer. Next Spring a layer of conidia is produced on the gall. During the second Fall the galls turn black and the initials of the ascomata develop. These mature and discharge ascospores in Spring, just two years after the initial infection.

KENDRICK: Doug Savile (1963, 1972) has pointed out that some of the fungi that occur in the arctic may take several years to produce mature fruit bodies because the growing season is so short.

LUTTRELL: Many fungi attacking logs may also take several years to fruit, and agarics growing in the soil may also require years to build up enough food reserves to permit fruiting.

Taxonomy vs. Ecology

PIROZYNSKI: Is there any correlation between taxonomic groupings and the conditions required for fruiting?

MÜLLER: We can't answer this question at present because so few examples have been worked out in full. We are fortunate to have reasonably full data on two species of *Talaromyces* and two of *Gnomonia*. As it happens, the two species of *Talaromyces* behave completely differently -- one is thermophilic, the other mesophilic. Even the two *Gnomonia* species behave rather differently. So I think the ecological adaptations fungi have undergone most probably override underlying taxonomic relationships.

DE HOOG: The ambrosia fungi are taxonomically as well as ecologically related, so similarities can exist in both areas.

KENDRICK: But most ecological groups are, in fact, taxonomically diverse. Dr. Webster will bring out an excellent example of this in the aquatic hyphomycetes. Perhaps I could mention a few other factors involved in induction of fruiting. A species of *Sordaria* is known to fruit only when its mycelium meets a physical obstacle, such as the wall of the petri dish. Injury and exposure to UV have also been used to induce fruiting.

MÜLLER: I didn't attempt to cover such factors because I thought they would over-extend the paper. Of course physical factors will have an effect, but I think I can say again that the responses are not uniform. Even the kind of inoculum used to start a culture can affect the manner of its ultimate fructification, as we found in *Talaromyces*, where cultures initiated by spread-out spore suspensions behaved differently from those in which the ino-

culum was older mycelium. The latter inoculum favoured sexual reproduction more than the former. We have no explanation for this, but it does show how careful you must be in experimental work to control all factors.

KENDRICK: Yes. Perhaps the only generalization we can make about factors involved in fruiting is that no generalizations are possible: at least, not yet. In my naiveté I originally asked Emil to prepare a paper entitled 'Mechanisms of phase change in fungi'. Sensibly, he said this was quite impossible -- we simply don't know enough about these biological switching mechanisms. Some fungi do it all for you -- free of charge. Other fungi are reluctant virgins, and yet others appear to have taken vows of chastity -- they are absolutely intractable. And so we cannot as yet, in many cases, accumulate the kind of data we need. All we can say is that evolution has, as usual, taken whatever stimuli were appropriate to a particular adaptation, and built them into the system. It appears that the trigger can be almost anything, but that it can also be so elaborately contrived as to elude our attempts to analyze or duplicate it.

We have now examined the anamorph-teleomorph problem in Ascomycetes from a number of different angles. The next chapter in some ways sums up what we know. It consists principally of extensive lists of connections, and it is the raw material from which future syntheses may be forged.....

17
Teleomorph-Anamorph Connections in Ascomycetes

B. Kendrick & F. DiCosmo with the Unitunicate and Bitunicate Committees of Kananaskis - II

> "The scientist looks for order in the appearances of nature...order does not display itself of itself; if it can be said to be there at all, it is not there for the mere looking...order must be discovered, and in a deep sense it must be created."
>
> J. Bronowski 1972.

INTRODUCTION

This is by far the largest chapter in the book, mainly because it incorporates the two lists of teleomorph-anamorph connections we have compiled for the unitunicate and the bitunicate Ascomycetes. But in addition to the lists themselves there are also reports from the two committees that were set up at Kananaskis-II to study and evaluate the lists, and there is an analysis of the various ways in which connections are established, and the different degrees of confidence that may be reposed in them. Since we have applied ratings derived from this analysis to our listings, we will begin by presenting the steps that led to the establishment of those ratings.

It is perfectly obvious that the connections reported in the literature vary widely in their degree of authenticity, all the way from a single report that a teleomorph and an anamorph had been seen associated on the natural substrate (without any confirmatory data or specimens), to a connection repeatedly proven in pure culture by the development of one morph from the other, or the development of both morphs simultaneously, from single spore inocula. In the best of all possible worlds, the actual material studied would be deposited in a major herbarium as voucher specimens which would permit proper up-dating of the taxonomy involved. This, of course, brings up the question of identification. A connection made twenty or more years ago, between an Ascomycete and its coelomycetous anamorph, in all probability cites an incorrect anamorph-generic name for the Coelomycete, since the taxonomy of the Coelomycetes was shrouded in all-but-complete darkness at that time. Even if an illustration accompanied the citation, it would in all probability not be adequately diagnostic by today's standards. In any case, an expert in teleomorphs is often poorly equipped to identify the anamorphs, and vice versa. But all of these problems can ultimately be solved

by the refinement of taxonomy and by the repetition of observations, though both of these processes will take time.

Although these thoughts and others like them were in all our minds at Kananaskis-II, it was Dr. Carmichael who performed the initial analysis and synthesis. He drew up a list of eight kinds of evidence for connections between anamorphs and teleomorphs, as follows:

1. Connection reported but evidence not given.
2. Forms found together once.
3. Forms found together frequently or regularly.
4. Forms found together frequently or regularly and architecture and/or spore morphology similar.
5. Forms found together with hyphal connections between the two.
6. Anamorph grown in culture from the teleomorph.
7. Anamorph grown in single ascospore or basidiospore cultures.
8. Both states developing in isolates derived from single spores or from mated single spore isolates.

The higher the number, the more reliable the connection. Spurred on by this, Drs. Weresub and Pirozynski subsequently produced a refined scheme, given below, which is the one we have applied to our lists.

EVIDENCE FOR AFFILIATION BETWEEN ANAMORPH & TELEOMORPH

1. UNDOCUMENTED: i.e., data inadequate for verifying determination of both partners.

2. DOCUMENTED: i.e., data sufficient for verifying determination of both partners: illustrations of both, descriptions of both, voucher specimens cited.

    1. CASUAL: Affiliation reported, but without circumstantial or experimental evidence given.
    2. CIRCUMSTANTIAL:
        1. Single observation of co-habitation.
        2. Frequent observation of regular co-habitation.
        3. Frequent observation of regular co-habitation, plus morphological similarity.
        4. Observation of co-habitation with organic connection.
    3. EXPERIMENTAL
        1. One morph produced in cultured isolate from the other.
        2. One morph produced in culture from single-spore isolate of the other.
        3. Holomorph produced from single-spore or mated culture of either morph.

POSSIBLE CODES:		
	1.1	2.1.
	1.2.1.	2.2.1.
	1.2.2.	2.2.2.
	1.2.3.	2.2.3.
	1.2.4.	2.2.4.
	1.3.1.	2.3.1.
	1.3.2.	2.3.2.
	1.3.3.	2.3.3.

Since we suspect that, in general, and for historic reasons, the teleomorphs in our list have been identified more accurately than the anamorphs; and since the teleomorphic name is automatically applicable to the holomorph (our holy grail), we have compiled our lists from the point of view of the teleomorph. Thus it is the teleomorphic names which are alphabetically arranged in our main listing, and the teleomorphic orders that are stressed in our condensed lists. The reader should consult Dr. Luttrell's experimental arrangement of anamorphs (Chapter 15) for a look at the other side of the story.

We decided to list connections for unitunicate and bitunicate Ascomycetes separately, since we believe that the differences between these groups stem from an evolutionary dichotomy that took place millions of years ago. This decision was also logistically felicitous, since one, gigantic, over-all list would have been extremely difficult to comprehend in its entirety, and might discourage mycologists from attempting the analyses and syntheses that are so urgently needed. The main listing gives binomials for both teleomorph and anamorph where these are available, and gives every connection we could find for every genus listed, with one or more appropriate references (which are given in full in the reference section at the end of the book).

But the lists are long, and an alphabetic arrangement is not necessarily ideal for all information retrieval purposes. Accordingly, we compiled two further, much more condensed lists, in which the teleomorphic generic names are arranged by Order according to the system enunciated in The Fungi, Vol. IVA, then alphabetically by family within each order, and alphabetically by genus within each family. Although this scheme is not necessarily followed elsewhere in the book -- the Conference was designed to encourage heterodox views and classificatory experiments -- it is a reasonable reference point, and the original volume is available to most students of mycology. In each of the subsidiary lists, against each teleomorph generic name, we have given the anamorphic generic name(s) and the number of species of each that are said to be connected to species of the teleomorph genus. We hope that this condensed information will make the broad picture easier to grasp, and will perhaps help to reveal glaring inconsistencies and errors.

Our lists have been compiled from the literature. We know they are incomplete and replete with errors, but we hope that their publication will stimulate the mycological fraternity into a spate of revisionary activity such that a much more definitive version may be prepared in the relatively near future.

Each long list, then, is followed by a condensed list, which in turn is followed by the

report of the appropriate committee. In the case of the Unitunicate Committee, the dialogue that followed presentation of their report is also given, because it deals with matters of great relevance to all mycologists.

Since the teleomorphs in each of the main lists are alphabetically arranged, they have not been indexed. The anamorphic genera, however, are fully indexed at the end of volume 2.

TELEOMORPH - ANAMORPH CONNECTIONS

ALPHABETICALLY BY UNITUNICATE ASCOMYCETE GENUS

2.3.1	Acanthonitschkea coloradensis Cash & Dav.	
	= Acremonium sp.	Cash & Davidson (1940)
	Acanthostigmella thaxteri Linder	
	= Xenosporella thaxteri Linder	Linder (1929)
2.2.2	Acanthotheciella barbata (Pat.) Höhn.	
	= Ypsilonia sp.	Nag Raj (1977)
2.2.2	A. mirabilis (Höhn.) Höhn.	
	= Ypsilonia mirabilis (Speg.) Nag Raj	Nag Raj (1977)
2.2.2.	A. tropicalis Nag Raj	
	= Ypsilonia tropicalis Nag Raj	Nag Raj (1977)
	Acrospermum compressum Tode ex Fries	
	= Dactylaria sp.	Webster (1956)
	A. gramineum Lib.	
	= Virgariella vel aff.	Webster (1956)
2.3.1	Ajellomyces dermatitidis McDon. & Lewis	
	= Chrysosporium sp. (Blastomyces dermatitidis Gilchrist & Stokes)	McDonough & Lewis (1968)
	Albertiniella polyporicola (Jacz.) Mall. & Cain	
	= Acremonium sp.	Malloch & Cain (1972)
	Amorphotheca resinae Parb.	
	= Sorocybe resinae de Vries	Parbery (1969)
	Amorphotheca sp.	
	= Hormoconis sp.	Carmichael et al. (1979)
2.2.1	Amphisphaeria argentinensis Nag Raj	
	= Bleptosporium pleurochaetum (Speg.) Sutt.	Nag Raj (1977b)
	A. incrustans Ell. & Ev.	
	= Dendryphiopsis atra (Cda.) Hughes	Hughes (1958), Ellis (1971)
	Anixiopsis sp.	
	= Chrysosporium sp.	Arx (1974)
	Arthrocobia sp.	
	= [?] Scytalidium sp.	Carmichael et al. (1979)
1.1	Anthostoma decipiens Nits.	
	= Cytospora decipiens Sacc. (=Naemospora sp., fide Grove (1935))	Grove (1935)
	[?] Anthostoma sp.	
	= Agaricostilbum palmicola Wright	Wright (1970)
1.1	Anthostomella taxi Grove	
	= Cryptocline taxicola (All.) Petr.	Grove (1935)
2.3.1	Aphanoascus cinnabarinus Zukal	
	= Chrysosporium sp.	
	= Paecilomyces cinnabarinus Jong & Davis	Jong & Davis (1975)

2.3.1	A. citrinus Malloch & Cain = Chrysosporium sp.	Malloch & Cain (ined.)
2.3.1	A. fulvescens (Cooke) Apinis = Chrysosporium sp.	
2.3.1	A. reticulisporus (Rout.) Malloch & Cain = Chrysosporium sp.	Malloch & Cain (ined.)
2.3.1	A. russuloides Malloch & Cain = Chrysosporium sp.	Malloch & Cain (ined.)
2.3.1.	Apinisia graminicola La Touche = Chrysosporium vel aff. fide Di Cosmo	La Touche (1968)
2.3.1.	A. queenslandica Apinis & Rees = Chrysosporium queenslandica Apin. & Rees	Apinis & Rees (1976)
	Apiocrea chrysosperma (Tul.) Syd. = Sepedonium chrysospermum (Bull.) Link	Petch (1938)
	A. tulasneana (Plowright) Petch = chlamydospores = [?] Sepedonium tulasneanum Sacc.	Petch (1938)
2.2.2.	Apiognomonia errabunda (Rob.) Höhn. = Colletotrichum sp. on living leaves; Discula sp. on stems; Sporonema sp. on dead leaves.	Wehmeyer (1975)
2.3.1.	Apioporthe verpis (De Lacroix) Wehmeyer = Phomopsis verpis (Sacc.) Höhn.	Wehmeyer (1933,1975)
	Apiosordaria verruculosa (Jensen) Arx. & Gams = Cladorrhinum foecundissimum Sacc. & Marchal.	Udagawa & Furuya (1972)
2.3.1.	Apiospora camptospora Penz. & Sacc. = Pteroconium sp. (=Papularia vinosa (Berk. & Curt.) Mason)	Ellis (1971), Hudson & McKenzie (1976)
2.3.1.	A. montagnei Sacc. = Arthrinium sp. (=Papularia arundinis (Corda) Fr.)	Ellis (1971)
2.2.2.	Apodospora simulans Cain & Mirza = unnamed phialidic hyphomycete	Cain & Mirza (1970)
2.2.2.	A. viridis Cain & Mirza = unnamed phialidic hyphomycete	Cain & Mirza (1970)
1.1.	Aporhytisma urticae Höhn. = Apomelasmia urticae Grove	Grove (1937)
2.3.1	Arachniotus albicans Apinis = Acladium vel aff.	Apinis (1964)
2.3.1	A. aureus (Eidam) Schroeter = Geotrichum vel aff.	Apinis (1964)
2.3.1	A. flavoluteus Kuehn & Orr = Oidiodendron sp.	Müller & Pacha-Aue (1968)
2.3.1	A. hyalinosporus (Kuehn, Orr & Ghosh) Apinis = unnamed arthric hyphomycete	Apinis (1964)
2.3.1	A. purpureus Müller & Pacha-Aue = Scopulariopsis sp.	Müller & Pacha-Aue (1968)
2.3.1	A. ruber (van Tieghem) Schroeter = unnamed arthric hyphomycete	
2.3.1.	Arachniotus sp. = Chrysosporium sp.	Udagawa & Takada (1968)
2.3.1	Arachnotheca glomerata (Müller & Pacha-Aue) Arx = Arthrographis sp.	Müller & Pacha-Aue (1966)
	Arnium calymmatosporum Jeng & Krug = Cladorrhinum sp.	Jeng & Krug (1977)
2.3.1.	Arthroderma benhamiae Ajello & Cheng = Trichophyton mentagrophytes (Robin) Blanchard	Rippon (1975)
2.3.1.	A. ciferri Var. & Ajello = Trichophyton georgiae Var. & Ajello	Rippon (1975)
2.3.1	A. curreyi Berkeley = Chrysosporium sp.	Apinis (1964)

2.3.1.	A. cuniculi Dawson	
	= Chrysosporium sp.	Apinis (1964)
2.3.1.	A. gertleri Bohme	
	= Trichophyton vanbreuseghemii Rioux, Jarry & Juminer	Rippon (1975)
2.3.1.	A. gloriae Ajello & Cheng	
	= Trichophyton gloriae Ajello & Cheng	Rippon (1975)
2.3.1.	A. lenticularum Pore, Tsae & Plunk.	
	= Trichophyton terrestre Durie & Frey	Rippon (1975)
2.3.1.	A. quadrifidum Dawson & Gentles	
	= Trichophyton terrestre Durie & Frey	Rippon (1975)
2.3.1.	A. simii Stockdale, MacKenzie & Austw.	
	= Trichophyton simii (Pinoy) Stockd., MacKenzie & Austw.	Rippon (1975)
2.3.1.	A. tuberculatum Kuehn	
	= chlamydospores	Apinis (1964)
2.3.1.	A. uncinatum Dawson & Gentles	
	= Keratinomyces ajelloi Vanbr.	Apinis (1964), Rippon (1975)
	Ascobolus bistisii Gamundi & Ranalli	
	= 'oidia'	van Brummelen (1967)
	A. furfurascens Pers. ex Hook	
	= Monilia sp.	Tubaki (1958)
	A. immersus Pers. ex Pers.	
	= [?] Stemphylium vel aff.	van Brummelen (1967)
	A. scatigenus (Berk.) Brumm.	
	= Papulaspora magnifica Hotson	Dodge (1920)
	A. stercorarius Rehm ex Bull.	
	= Monilia sp.	Tubaki (1958)
	Ascocalvatia alveolata Malloch & Cain	
	= arthric hyphomycete	Malloch & Cain (1970)
	Ascocalyx abietis Naumov	
	= Bothrodiscus berenice (Berk. & Curt. in Berk.) Groves	Groves (1968)
	A. laricina (Ettlinger) Schlapfer	
	= Brunchorstia laricina Ettlinger	
	A. tenuisporus Groves	
	= Bothrodiscus sp.	Groves (1968), Shaw (1973)
	Ascocorticium anomalum (Ell. & Harkn.) Earle	
	= Acrodontium sp.	de Hoog (1972)
	Ascocoryne sarcoides (Jacq. ex Gray) Groves & Wils.	
	= Coryne dubia (Pers.) S.F. Gray	Groves & Wilson (1967)
2.3.1.	Ascodichaena rugosa Butin	
	= Polymorphum rugosum (Fr.) D. Hawksworth & Punith.	Butin (1977)
	Ascophanus testaceus (Moug. in Fr.) Phillips	
	= Oedocephalum sp.	Tubaki (1958)
	Ascorhiza leguminosarum Lechtova-Trnka	
	= terminal chlamydospores	Malloch (1970)
2.2.2.	Ascotricha amesii Hawksworth	
	= Dicyma sp.	Hawksworth (1971)
2.2.2.	A. amphitricha (Corda) Hughes	
	= Dicyma sp.	Hawksworth (1971)
2.2.2.	A. arcuata Ames	
	= Dicyma sp.	Ames (1963)
2.2.2.	A. bosei D. Hawksworth	
	= Dicyma sp.	Hawksworth (1971)
2.2.2.	A. chartarum Berk.	
	= Dicyma ampullifera Boul.	Ellis (1971)
2.2.2.	A. congoensis Ames	
	= Dicyma sp.	Ames (1963)
2.2.2.	A. erinacea Zambet.	
	= Dicyma sp.	Hawksworth (1971)
2.2.2.	A. guamensis Ames	
	= Dicyma sp.	Ames (1963)

2.2.2.	A. lusitanica R. Kenn.	
	= Dicyma sp.	Hawksworth (1971)
2.2.2.	A. pusilla (Ell. & Ev.) Chivers	
	= Dicyma sp.	Ames (1963)
2.2.2.	A. xylina Ames	
	= Dicyma sp.	Ames (1963)
2.2.2.	Atropellis pinicola Zeller & Gooding	
	= Neofuckelia pinicola Zeller & Good.	Zeller & Gooding (1930), Shaw (1973)
	A. piniphila (Weir) Lohman & Cash	
	= Fuckelia sp.	Korf (1973)
2.3.1.	Auxarthron conjugatum (Kuehn) Orr & Kuehn	
	= Malbranchea sp.	Sigler & Carmichael (1976)
	Balansia claviceps Speg.	
	= Ephelis sp.	Ullasa (1969)
	B. pallida Wint. in Rabenh.	
	= Ephelis sp.	
	Belonidium albidum Grel. & Croz.	
	= Chalara vel aff.	Grelet & Crozals (1951)
	Belonopsis eriacae (Roll.) Aebi	
	= Cystodendron sp.	Aebi (1972)
	B. mediella (Karst.) Aebi	
	= Cystodendron sp.	Aebi (1972)
2.2.1.	Biostictis chroodiscoides Sherwood	
	= Rhinocladiella vel aff.	Sherwood (1978)
2.2.1.	B. psychotriae (Mont.) Sherwood	
	= Cylindrocarpon sp. (as Fusidium violaceum Pat.)	Petrak (1950), Sherwood (1977)
2.3.1.	Bisporella discedens (Karst.) Carpenter	
	= Cystodendron sp.	Carpenter (1975)
	Blogiascospora marginata (Fuckel) Shoem., Müll. & Morgan-Jones	
	= Seiridium marginatum Nees ex Steud.	Müller & Morgan-Jones (1966)
2.3.1.	Blumeriella jaapii (Rehm.) Arx	
	= Phloeosporella padi (Lib.) Arx	Arx (1974)
	= Phloeosporella ceanothi (Ell. & Ev.) Höhn.	
	Bombardia lunata Zickler	
	= Phialophora vel aff.	Tubaki (1958)
2.3.1.	Botryoascus synnaedendrus (van der Walt & Scott) Arx	
	= Raffaelea vel aff.	Arx et al. (1977)
2.3.1.	Botryotinia convoluta (Drayton) Whetzel	
	= Botrytis convoluta Whetz. & Drayton	Whetzel & Drayton (1932), Hennebert (1973)
2.3.1.	B. fuckeliana (de Bary) Whetz.	
	= Botrytis cinerea Pers. ex Fr.	Groves & Loveland (1953)
2.3.3.	B. porri van Beyma	
	= Botrytis porri (van Beyma) Buchw.	Elliott (1964)
2.3.1.	B. ricini (Godfrey) Whetz.	
	= Amphobotrys ricini (Buchw.) Henneb.	Whetzel (1945), Hennebert (1973)
	B. squamosa Viennot-Bourgin	
	= Botrytis squamosa Walker	Bergquist & Lorbeer (1972)
2.3.1.	Broomella actua Shoem. & Müll.	
	= Pestalotia truncata Lév.	Shoemaker & Müller (1963)
2.3.1.	B. excelsa Shoem. & Müller	
	= Pestalotia excelsa (Petr.) Shoem. & Müll.	Shoemaker & Müller (1963)
2.3.1.	B. montaniensis (Ell. & Ev.) Müller & Ahmad	
	= Pestalotia pestalozzioides (Dearn. & Fairm. in Fairman) Shoem. & Müll.	Shoemaker & Müller (1963)
2.3.1.	B. vitalbae (Berk. & Br.) Sacc.	
	= Monotrichum sp.	
	= Pestalotia vitalbae Shoem. & Müll.	Shoemaker & Müller (1963), Müller (1971)
2.3.1.	Byssoascus striatosporus (Barron & Booth) Arx	
	= Oidiodendron sp.	von Arx (1974)

2.3.1.	Byssochlamys fulva Olliver & Smith	
	= Paecilomyces fulvus Stolk & Samson	Stalk & Samson (1971), Samson (1974)
2.3.1.	B. nivea Westling	
	= Paecilomyces niveus Stolk & Samson	Benjamin (1956), Stolk & Samson (1971), Samson (1974)
2.3.1.	B. verrucosa Samson & Tansey	
	= Paecilomyces verrucosus Samson & Tansey	Samson & Tansey (1975)
2.3.1.	B. zollerniae Ram.	
	= Paecilomyces zollerniae Stolk & Samson	Stolk & Samson (1971), Samson (1974)
2.3.1.	Byssostilbe stilbigera (B. & Br.) Petch	
	= Stilbella tomentosa (Schrad. per Grev.) Bres.	Gams (1971), Carmichael et al. (1979)
	= Tilachlidium sp.	
	Callorina fusarioides (Berk.) Korf	
	= Cylindrocolla urticae (Pers.) Bon.	Lindau (1907)
2.2.2.	Calloriopsis gelatinosa (Ell. & Mart.) H. & P. Sydow	
	= Eriomycopsis minima Hansf.	Hansford (1942), Deighton & Pirozynski (1972)
	Calonectria cephalosporii Hansf.	
	= Acremonium sp.	Gams (1971)
	C. colhounii Peer.	
	= Cylindrocladium colhounii Peerally	Peerally (1974)
	C. crotalariae (Loos) Bell & Sobers	
	= Cylindrocladium crotalariae (Loos) Bell & Sobers	Peerally (1974)
	C. diploa (B. & C.) Wollenw.	
	= Fusarium juruanum P. Henn.	Booth (1974)
	C. hederae Booth & Murray	
	= Cylindrocladium hederae (Arn.) Peer.	Peerally (1974)
	C. ilicicola Boed. & Reitsma	
	= Cylindrocladium ilicicola (Hawley) Boedijn & Reitsma	
	C. kyotensis Terashita	
	= Cylindrocladium sp.	Terashita (1968)
	C. quinqueseptata Figueir. & Namek.	
	= Cylindrocladium quinqueseptatum Boed. & Reits.	
	C. reteaudii (Bugn.) Booth	
	= Cylindrocarpon reteaudii Bugn.	Booth (1966)
	C. rigidiuscula (Berk. & Br.) Sacc.	
	= Fusarium decemcellulare Brick	Booth (1959,1971), Booth & Waterston (1964)
	C. theae Loos.	
	= Cylindrocladium theae (Petch) Subram.	
	C. ukolayii Thaung	
	= Cylindrocarpon ukolayii Thaung	Thaung (1976)
2.3.1.	Caloscypha fulgens (Pers.) Boud.	
	= Geniculodendron pyriforme Salt	Paden (1972), Conway (1975), Paden, Sutherland & Woods (1978)
	Calostilbe calostilbe Höhn.	
	= Calostilbella sp.	Morris (1963)
	C. striispora (Ell. & Ev.) Seaver	
	= Calostilbella sp.	Seaver (1929)
	Calycellina carolinensis Nag Raj & Kendr.	
	= Chaetochalara aspera Piroz. & Hodges	Nag Raj & Kendrick (1975)
	Cenangium populneum (Pers.) Rehm	
	= Chondroplea populea (Sacc. & Briard) Kleb.	Hedgcock & Hunt (1916)
	C. ferruginosum Fr. ex Fr.	
	= Brunchorstia pinea (Karst.) Höhn.	Vloten & Gremmen (1953)

	Cephalotheca savoryi Booth	
	= Tritirachium sp.	Booth (1961)
	C. sulfurea Fuckel	
	= Acremonium vel aff.	
	= Paecilomyces sp.	Tubaki (1958), Udagawa & Horie (1971)
2.3.1.	Ceratocystiopsis minuta (Siem.) Upadh. & Kendr.	
	= Sporothrix vel aff.	Upadhyay & Kendrick (1975)
2.3.1.	C. minuta-bicolor (Davids.) Upadh. & Kendr.	
	= Hyalorhinocladiella sp.	Upadhyay & Kendrick (1975)
2.3.1.	Ceratocystis abiocarpa Davidson	
	= Leptographium sp.	Davidson (1966)
2.3.1.	C. adiposa (Butl.) C. Moreau	
	= Chalara sp.	Nag Raj & Kendrick (1975)
2.3.1.	C. aequivaginata Olchow. & Reid	
	= Verticicladiella vel aff.	Olchowecki & Reid (1974)
2.3.1.	C. arborea Olchow. & Reid	
	= Pesotum sp.	Olchowecki & Reid (1974)
2.3.1.	C. angusticollis Wright & Griffin	
	= Sporothrix vel aff.	Olchowecki & Reid (1974)
2.3.1.	C. autographa Bakshi	
	= Chalara sp.	Nag Raj & Kendrick (1975)
2.3.1.	C. brevicollis Davids.	
	= Verticicladiella sp.	Davidson (1958)
2.3.1.	C. brunneociliata (Math.-Kaarik) Hunt	
	= Pesotum sp.	Hunt (1956)
2.3.1.	C. brunneocrinita Wright & Cain	
	= Hyalorhinocladiella vel aff.	Olchowecki & Reid (1974)
	C. californica Devay, Davids. & Moll.	
	= Hyalodendron sp.	
2.3.1.	C. cainii Olchow. & Reid	
	= Graphium sp.	Olchowecki & Reid (1974)
2.3.1.	C. cana (Münch) C. Moreau	
	= Pachnodium canum Upadh. & Kendr.	Upadhyay & Kendrick (1975)
2.3.1.	C. capitata Griffin	
	= Sporothrix vel aff.	Griffin (1968)
2.3.1.	C. clavata (Math.) Hunt	
	= Graphium vel aff.	Hunt (1956)
2.3.1.	C. coerulescens (Münch) Bakshi	
	= Chalara ungeri Sacc.	Nag Raj & Kendrick (1975)
2.3.1.	C. columnaris Olchow. & Reid	
	= Phialographium sp.	Olchowecki & Reid (1974)
2.3.1.	C. concentrica Olchow. & Reid	
	= blastic-sympodial Hyphomycete	Olchowecki & Reid (1974)
2.3.1.	C. conicollis Olchow. & Reid	
	= Hyalorhinocladiella vel aff.	Olchowecki & Reid (1974)
2.3.1.	C. coronata Olchow. & Reid	
	= Sporothrix vel aff.	Olchowecki & Reid (1974)
2.3.1.	C. crenulata Olchow. & Reid	
	= Hyalorhinocladiella vel aff.	Olchowecki & Reid (1974)
2.3.1.	C. curvicollis Olchow. & Reid	
	= Verticicladiella vel aff.	Olchowecki & Reid (1974)
2.3.1.	C. davidsonii Olchow. & Reid	
	= Phialographium sp.	Olchowecki & Reid (1974)
2.3.1.	C. deltoidiospora Olchow. & Reid	
	= blastic-sympodial Hyphomycete	Olchowecki & Reid (1974)
2.3.1.	C. dolominuta Griffin	
	= Pesotum vel aff.	Olchowecki & Reid (1974)
2.3.1.	C. dryocoetidis Kendr. & Moln.	
	= Verticicladiella dryocoetidis Kendr. & Moln.	Kendrick & Molnar (1965)

2.3.1.	C. europhioides Wright & Cain = [?] Leptographium sp.	Olchowecki & Reid (1974)
2.3.1.	C. fasciata Olchow. & Reid = Hyalorhinocladiella vel aff.	Olchowecki & Reid (1974)
2.3.1.	C. fagacearum (Bretz) Hunt = Chalara quercina Henry	Hunt (1956), Nag Raj & Kendrick (1975)
2.3.1.	C. fimbriata Ellis & Halst. = Chalara sp.	Nag Raj & Kendrick (1975)
2.3.1.	C. floccosa (Mathiesen) Hunt = [?] Graphium silanum Goid.	Goidanich (1936), Hunt (1956)
2.3.1.	C. galeiformis Bakshi = Acremonium vel aff. = Leptographium vel aff.	Hunt (1956)
2.3.1.	C. huntii Robins.-Jeff. = Leptographium sp.	Robinson-Jeffrey & Grinchenko (1964)
2.3.1.	C. introcitrina Olchow. & Reid. = Hyalopesotum introcitrina Upadh. & Kendr.	Upadhyay & Kendrick (1975)
2.3.1.	C. ips (Rumb.) C. Moreau = Graphilbum sp. = Trichosporon	Goidanich (1936), Hunt (1956)
2.3.1.	C. leptographioides (Davids.) Hunt = Leptographium sp.	Hunt (1956)
2.3.1.	C. longispora Olchow. & Reid = blastic-sympodial Hyphomycete	Olchowecki & Reid (1974)
2.3.1.	C. major (van Beyma) C. Moreau = Graphium vel aff.	Hunt (1956)
2.3.1.	C. megalobrunnea Davids. & Tooke = Yeast-like (? Sporothrix)	
2.3.1.	C. minima Olchow. & Reid = Verticicladiella vel aff.	Olchowecki & Reid (1974)
2.3.1.	C. minor (Hedgc.) Hunt = Hyalorhinocladiella sp.	Olchowecki & Reid (1974)
2.3.1.	C. moniliformis (Hedgc.) C. Moreau = Chalara sp.	Nag Raj & Kendrick (1975)
2.3.1	C. multiannulata (Hedgc. & Davids.) Hunt = Hyalodendron sp.	
2.3.1	C. nigra Davids. = Verticicladiella sp. fide Kendrick & DiCosmo = Acremonium sp.	Davidson (1950)
2.3.1.	C. obscura (Davids.) Hunt = Graphium vel aff.	Hunt (1956)
2.3.1.	C. olivacea (Mathiesen) Hunt = Phialographium sp.	Hunt (1956)
2.3.1.	C. olivaceapinii Davids. = Graphium sp.	
2.3.1.	C. ossiformis Olchow. & Reid = Graphium sp.	Olchowecki & Reid (1974)
2.3.1.	C. pallidobrunnea Olchow. & Reid = Verticicladiella vel aff.	Olchowecki & Reid (1974)
2.3.1.	C. paradoxa (Dade) C. Moreau = Chalara paradoxa (de Seynes) Sacc.	Nag Raj & Kendrick (1975)
2.3.1.	C. parva Olchow. & Reid = Verticicladiella vel aff.	Olchowecki & Reid (1974)
2.3.1.	C. penicillata (Grosm.) C. Moreau = Verticicladiella penicillata (Grosm.) Kendr.	Kendrick (1962)
2.3.1.	C. perfecta Davids. = blastic-sympodial Hyphomycete	Olchowecki & Reid (1974)
2.3.1.	C. perparvispora Hunt = [?] Sporothrix vel aff.	Davidson (1942), Hunt (1956)

2.3.1.	C. piceae (Münch) Bakshi = Pesotum piceae Crane & Schokn.	Crane & Schoknecht (1973)
2.3.1.	C. piceaperda (Rumb.) C. Moreau = Leptographium sp.	Hunt (1956)
2.3.1.	C. pilifera (Fr.) C. Moreau = Hyalodendron sp. = Sporothrix sp.	Griffin (1968), de Hoog (1974)
2.3.1.	C. polonicum (Siem.) C. Moreau = Leptographium sp.	Hunt (1956)
2.3.1.	C. populicola Olchow. & Reid = Sporothrix sp.	Olchowecki & Reid (1974)
2.3.1.	C. pseudoeurophioides Olchow. & Reid = Verticicladiella sp.	Olchowecki & Reid (1974)
2.3.1.	C. pseudominor Olchow. & Reid = blastic-sympodial Hyphomycete	Olchowecki & Reid (1974)
	C. radicicola (Bliss) C. Moreau = Chalara sp.	Nag Raj & Kendrick (1975)
2.3.1.	C. rostrocylindrica (Davids.) Hunt = Leptographium sp.	Hunt (1956)
2.3.1.	C. sagmatospora Wright & Cain = Phialographium sagmatosporae Upadh. & Kendr.	Upadhyay & Kendrick (1975)
2.3.1.	C. serpens (Goid.) G. Moreau = Leptographium sp.	Hunt (1956)
2.3.1.	C. sparsa Davids. = Graphilbum sparsum Upadh. & Kendr.	Upadhyay & Kendrick (1975)
2.3.1.	C. spinifera Olchow. & Reid = Hyalorhinocladiella vel aff.	Olchowecki & Reid (1974)
2.3.1.	C. spinulosa Griffin = Hyalorhinocladiella vel aff.	Olchowecki & Reid (1974)
	C. tenella Davids. = Sporothrix vel aff. fide DiCosmo ined.	Davidson (1958)
2.3.1.	C. torticillata Olchow. & Reid = Pesotum sp.	Olchowecki & Reid (1974)
2.3.1.	C. tubicollis Olchow. & Reid. = Hyalorhinocladiella sp.	Olchowecki & Reid (1974)
2.3.1.	C. ulmi (Buism.) C. Moreau = Pesotum ulmi (Schwartz) Crane & Schokn.	Crane & Schoknecht (1973)
	Ceriosporopsis circumvestita (Kohlm.) Kohlm. = chlamydospores	Kohlmeyer (1972)
	C. halima Linder = chlamydospores	Kohlmeyer (1972)
2.2.2.	Chadefaudia marina G. Feldmann = unnamed coelomycete (pycnidial)	Kohlmeyer (1973)
2.3.1.	Chaetomium piluliferum Daniels = Botryotrichum piluliferum Sacc. & March.	Daniels (1961)
2.2.2.	C. semispirale Udagawa & Cain = Humicola sp.	Udagawa & Cain (1970)
2.3.1.	C. trigonosporum (Marchal) Chivers. = Scopulariopsis sp.	Udagawa (1970)
	Chaetomium sp. = Papulaspora sp. = Trichocladium sp.	Carmichael, Kendrick & Conners (1979)
2.3.1.	Chaetosartorya chrysella (Kwon & Fennell) Subram. = Aspergillus chrysellus Kwon & Fennell	Subramanian (1972), Malloch & Cain (1972)
2.3.1.	C. cremea (Kwon & Fennell) Subramanian = Aspergillus cremeus Kwon & Fennell	
2.3.1.	C. stromatoides Wiley & Simmons = Aspergillus stromatoides Raper & Fennell	Wiley & Simmons (1973)
	Chaetosphaerella fusca (Fckl.) Müller & Booth = Oedemium didymum (Schw.) Hughes	Hughes & Hennebert (1963), Müller & Booth (1972)

	C. phaeostroma (Dur. & Mont) Booth & Müller	
	= Oedemium minus (Link) Hughes	Hughes & Hennebert (1963), Müller & Booth (1972)
	= Phialocephala sp.	
2.2.2.	Chaetosphaeria brevispora Shoem.	
	= Zanclospora brevispora Hughes & Kendr.	Hughes & Kendrick (1965)
2.3.1.	C. callimorpha (Mont.) Sacc.	
	= Codinaea sp.	Booth (1957), Hughes & Kendrick (1965)
2.2.2.	C. cupulifera (B. & Br.) Sacc.	
	= Catenularia cuneiformis (Rich.) Mason	Hughes (1965)
2.2.2.	C. dingleyae Hughes, Kendr. & Shoem.	
	= Codinaea sp.	Hughes & Kendrick (1968)
2.2.2.	C. fusca Fckl.	
	= Cladotrichum sp.	Hughes (1953)
2.3.1.	C. innumera Tul.	
	= Catenularia sp.	Booth (1957), Müller (1971)
	= Chloridium sp.	
2.3.1.	C. myriocarpa (Fr.) Booth	
	= Catenularia heimii Mang.	Booth (1957), Müller (1971)
	= Chloridium sp.	
2.2.2.	C. novae-zelandiae Hughes & Shoem.	
	= Catenularia sp.	Hughes (1965)
	C. phaeostroma (Dur. & Mont.) Fckl.	
	= Cladotrichum triseptatum B. & Br.	Hughes (1953)
	C. pomiformis (Fr. ex Fr.) Müller	
	= Stachybotrys sp.	Booth (1957), Müller (1957)
2.2.2.	C. pulchriseta Hughes, Kendr. & Shoem.	
	= Codinaea sp.	Hughes & Kendrick (1968)
2.3.1.	C. pulviscula (Curr.) Booth	
	= Menispora caesia Pr.	Booth (1957), Hughes & Kendrick (1963)
2.2.2.	C. talbotii Hughes, Kendr. & Shoem.	
	= Codinaea sp.	Hughes & Kendrick (1968)
2.3.1.	Chlorociboria aeruginascens (Nyl.) Kan. ex Ram., Korf & Batra, subsp. aeruginascens Dixon	
	= Dothiorina tulasnei (Sacc.) Höhn.	Dixon (1975)
2.3.1.	C. aeruginascens (Nyl.) Kan. ex Ram., Korf & Batra subsp. brasiliensis (B. & C.) Dixon	
	= Dothiorina tulasnei (Sacc.) Höhn.	Dixon (1975)
2.3.1.	Ciboria acerina Whetz. & Buchw.	
	= Botrytis sp. vel aff.	Dennis (1956), Arx (1970)
	= Myrioconium sp. (spermatial)	
	Ciborina whetzelii (Seav.) Seav.	
	= Sclerotium bifrons Ell. & Ev.	Shaw (1973)
2.2.2.	Claussenomyces atrovirens (Pers. ex Pers.) Korf & Abawi	
	= ascospores bud in the ascus	Dennis (1968)
	C. prasinulus (Karst.) Korf & Abawi	
	= Dendrostilbella prasinula Höhn.	Korf (1973), Dennis (1968)
2.2.2.	C. pseudotsugae (Groves) Ouellette & Piroz.	
	= Sirodothis vel aff.	
	or = Pragmopycnis vel aff.	Groves (1952), Ouellette & Pirozynski (1974)
	Claviceps nigricans Tul.	
	= Sphacelia nigricans Sacc.	
	= Sclerotium nigricans Sacc.	
2.3.1.	C. purpurea (Fr.) Tul.	
	= Sphacelia segetum Lév.	Arx (1970)
	Cleistoiodophanus sp?	
	= Oedocephalum sp.	Carmichael, Kendrick & Conners (1979)
2.2.2.	Coccomyces coronatus de Not.	
	= Leptothyrium botryoides Sacc.	
	= L. discosioides Niessl	
	= Schizothyrella quercina Thüm.	Grove (1937)

2.2.2.	C. dentatus Sacc.	
	= Leptothyrium quercinum Sacc.	Grove (1937)
	C. hiemalis Higg.	
	= Cylindrosporium hiemalis Higg.	
	= Septocyta sp.	Higgins (1914), Petrak (1939)
2.2.2.	C. laciniatus (Alb. & Schw.) Schroet.	
	= Leptothyrium sp.	Nannfeldt (1932)
	C. lutescens Higg.	
	= Cylindrosporium lutescens Higg.	Higgins (1914)
	C. prunophorae Higg.	
	= Cylindrosporium prunophorae Higg.	Higgins (1914)
2.2.2.	C. rubi Karst.	
	= Leptothyrium rubi Sacc.	Grove (1937)
	Coniochaeta elaeicola (Henn.) C. & M. Moreau	
	= Phialophora sp.	Moreau & Moreau (1949)
	C. leucoplaca (Berk. & Rav.) Cain	
	= Phialophora sp.	Cain (1961)
	C. ligniaria (Grev.) Mass.	
	= Phialophora sp.	Rogers (1965)
	C. malacotricha (Niessl) Trav.	
	= Phialophora sp.	von Arx (1970)
	C. tetraspora Cain	
	= Phialophora sp.	Cain (1961)
	Cordyceps clavulata (Schw.) Ell. & Ev.	
	= Hirsutella lecaniicola (Jaap) Petch	Petch (1948)
	C. entomorrhiza (Dicks.) Link	
	= [?] Hirsutella eleutheratorum (Nees) Petch	
2.2.1.	C. forquignoni Quél.	
	= Hymenostilbe muscaria Petch	Petch (1938)
	C. gracilis Mont. & Dr.	
	= Isaria dubia Delacr.	
2.3.1.	C. memorabilis Ces.	
	= Paecilomyces farinosus (Holm. ex S.F. Gray) Brown & Smith	
2.3.1.	C. militaris (L.) Link	
	= Acremonium sp.	Gams (1971)
2.3.1.	C. ophioglossoides (Ehrenb.) Link	
	= Verticillium sp.	Gams (1971)
	C. pistillariaeformis B. & Br.	
	= Hirsutella lecaniicola (Jaap) Petch	Petch (1948)
	C. sphecocephala (Klotz.) Cke.	
	= Hymenostilbe sphecophila (Ditm.) Petch	Petch (1937,1948)
	C. tuberculata (Leb.) Maire	
	= Akanthomyces sphingum (Schw.) Petch	Petch (1948)
	Cordyceps sp.	
	= Gibellula sp.	
	= Sphacelia sp.	Carmichael, Kendrick & Conners (1979)
2.3.1.	Corollospora pulchella Kohlm.	
	= Clavariopsis bulbosa Anast.	Shearer & Crane (1971)
	Crumenulopsis pinicola (Fr.) Groves	
	= Digitosporium piniphilum Gremm.	Groves (1969)
2.3.1.	C. sororia (Karst.) Groves	
	= Digitosporium piniphilum Gremm.	Gremmen (1953), Groves (1969)
2.2.2.	Cryptendoxyla hypophloia Mall. & Cain	
	= Chalara sp.	Nag Raj & Kendrick (1975)
2.3.1	Cryptodiaporthe auberti (West.) Wehm. var. comptoniae (Schw.) Wehm.	
	= [?] Pestalozzia flagellifera Ell. & Ev. (≡ Neobarclaya flagellifera (Ell. & Ev.) Kze. non N. flagellifera (Ell. & Ev.) Sacc.)	Wehmeyer (1933)
2.2.2.	C. aesculi (Fckl.) Petr.	
	= Discella aesculi (Cda.) Oud.	Arx (1970)

2.2.2.	C. castanea (Tul.) Wehm. = Discella sp. (Fusicoccum castaneum Sacc.)	Wehmeyer (1933), Arx (1970)
2.2.2.	C. galericulata (Fckl.) Wehm. = Malacostroma carneum (Thüm.) Höhn. (≡ Myxosporium carneum Thüm.)	Wehmeyer (1933)
2.2.2.	C. hystrix (Tode ex Fr.) Petr. = Discella acerina (Westd.)	Wehmeyer (1933), Arx (1970)
2.2.2.	C. konseiensis Kobay. = Hendersonula konseiensis Kobay.	Kobayasi (1962)
2.2.1.	C. lebiseyi (Desm.) Wehm. = Phomopsis lebiseyi (Sacc.) Died.	Wehmeyer (1933)
2.2.2.	C. populea (Fckl.) Butin = Chondroplea populea (Sacc. & Briard) Kleb.	Booth, Gibson & Sutton (1973)
2.3.1.	C. salicella (Fr.) Petr. = Discella salicis (Westd.) Boem.	Wehmeyer (1933), Boerema (1970)
2.3.1.	C. salicina (Curr.) Wehm. = [?] Discella carbonacea (Fr.) B. & Br.	Wehmeyer (1933)
2.2.1.	Cryptosphaeria eunomia (Fr.) Fckl. = Cytosporina millipunctata Sacc.	Grove (1935)
	C. populina (Pers.) Sacc. = Cytosporina sp.	Schreiner (1929)
1.1.	Cryptospora betulae Tul. = Cryptosporium betulinum Jaap	Grove (1937)
1.1.	C. suffusa Tul. = Cryptosporium neesii Corda	Grove (1937)
1.1.	Cryptosporella aurea Sacc. 1.1. = Cryptosporium amygdalinum Sacc. 1.1. = Cryptosporium betulinum Jaap.	Grove (1937)
1.1	C. hypodermia Sacc. = (?) Cytosporina ludibunda Sacc.	Grove (1937)
1.1	C. populina Sacc., (=[?] Cryptodiaporthe populina Petr.) = Cryptosporium coronatum Fckl. (=[?] Discella coronata Petr.)	Grove (1937)
2.3.1	Ctenomyces serratus Eidam = Chrysosporium sp.	Orr, Kuehn & Plunkett (1963)
2.3.1.	Dactylomyces crustaceus (Apin. & Chest.) Stolk = Paecilomyces sp.	Stolk (1965)
2.3.1.	D. thermophilus Sopp. = [?] Polypaecilum sp.	Apinis (1967)
2.3.1.	Daldinia angloensis (Wels. & Curr.) Sacc. = [?] Virgariella sp.	Miller (1930)
2.3.1.	D. concentrica (Bolt. ex Fr.) Ces. & de Not. = Nodulisporium sp.	Molliard (1904), Tubaki (1958)
2.2.2.	Darkera abietis Whit., Reid & Piroz. = Tiarosporella abietis Whit., Reid. & Piroz.	Whitney, Reid & Pirozynski (1975)
2.2.2.	D. parca Whit., Reid & Piroz. = Tiarosporella parca Whit., Reid, & Piroz.	Whitney, Reid & Pirozynski (1975)
2.3.1.	Dasyscypha corticalis (Pers. ex Fr.) Mass. = [?] Gliocladium sp.	Berthet (1964)
	D. pulveracea (Alb. & Schw. ex Fr.) Höhn. = [?] Cytospora sp.	Dennis (1949)
1.1	Debaryomyces sp. = Torulopsis sp.	Tubaki (1958)
2.3.1.	Dekkera bruxellensis van der Walt = Brettanomyces sp.	Arx (1970)
2.3.1.	D. intermedia van der Walt = Brettanomyces sp.	Arx (1970)
2.3.1	Dermea balsamea (Pk.) Seav. = Foveostroma abietinum (Pk.) DiCosmo	Dodge (1932), Groves (1946), DiCosmo (1978)
2.3.1	D. cerasi (Pers. ex Fr.) Fr. = Foveostroma drupacearum (Lév.) DiCosmo	Groves (1946), DiCosmo (1978)

2.3.1	D. grovesii Reid & Piroz.	
	= Cornicullariella abietis Karst.	DiCosmo (1978)
2.3.1	D. molliuscula (Schw.) Cash	
	= Gelatinosporium fulvum Pk.	Groves (1946)
2.3.1	D. padi Fr.	
	= Micropera padina Sacc.	Groves (1946)
2.3.1	D. tetrasperma Funk	
	= Micropera lunaspora (Linder) Funk	Funk (1976)
2.3.1	D. viburni Groves	
	= Cornicullariella hystricina (Ell.) DiCosmo	Groves (1946), DiCosmo (1978)
2.3.1	D. pseudotsugae Funk	
	= Micropera boycei (Dearn.) Groves	Funk (1976)
2.3.1	Desmazierella acicola Lib.	
	= Verticicladium trifidum Pr.	Gremmen (1949), Hughes (1951)
1.1.	Diachora onobrychidis Müll.	
	= Diachorella onobrychidis (DC. ex Fr.) Höhn.	Grove (1935)
1.1.	Diaporthe aculeata (Schw.) Sacc.	
	= Phomopsis phlyctaenoides (B. & C.) Höhn.	Wehmeyer (1933)
1.1.	D. adunca (Rob.) Niessl	
	= Phomopsis subordinaria (Desm.) Trav.	Wehmeyer (1933), Grove (1937)
2.2.2.	D. ambigua Nits.	
	= Phomopsis ambigua Trav.	Wehmeyer (1933), Grove (1937)
	= Phomopsis amelanchiers Gr.	
	[?] D. americana Speg.	
	= Phomopsis magnoliicola Died.	Wehmeyer (1933)
2.3.1.	D. ampelopsidis Ell. & Ev.	
	= Phomopsis ampelopsidis Petr.	Wehmeyer (1933), Grove (1937)
2.3.1	D. arctii (Lasch) Nits.	
	= Phomopsis ambigua (Sacc.) Trav.	Wehmeyer (1933)
	= Phomopsis arctii (Sacc.) Trav.	
2.2.2.	D. arctii (Lasch.) Nits. var achilleae (Auers.)	
	= Phomopsis achilleae (Sacc.) Höhn.	Wehmeyer (1933)
1.1.	D. asclepiadis Ell. & Ev.	
	= Phomopsis missouriensis Bub.	Wehmeyer (1933)
2.1.	D. asparagi Fckl.	
	= Phomopsis asparagi Grove	Grove (1937)
2.1.	D. aucubae Sacc.	
	= Phomopsis aucubae Trav.	Grove (1937)
2.2.2.	D. batatis Hart. & Field (≡D. phaseolorum (C. & E.) Sacc. var. batatis (Hart & Field) Wehm.	
	= Phomopsis batatae (Ell. & Halst.) Hart. & Field	Wehmeyer (1933)
2.2.2.	D. beckhausii Nits.	
	2.2.2. = Phomopsis beckhausii (Cke.) Trav.	
	2.1. = Phomopsis tinea Höhn.	Gilman, Tiffany & Lewis (1959)
2.1.	D. berkeleyi Nits. [Diaporthopsis angelicae Wehm. fide Grove 1937]	
	= Phomopsis asteriscus Gr.	
	= Phomopsis caulographa Gr.	
	= Phomopsis hysterula Gr.	Grove (1937)
1.1.	D. brachyceras Sacc.	
	= Phomopsis brachyceras Gr.	Wehmeyer (1933), Grove (1937)
1.1	D. carpini (Fr.) Fckl.	
	= Fusicoccum carpini Sacc.	Wehmeyer (1933)
1.1.	D. cinerascens Sacc.	
	= Phomopsis cinerascens (Sacc.) Trav.	Wehmeyer (1933), Grove (1937)
2.2.2.	D. circumscripta Otth.	
	= Phomopsis sambucina Trav. [P. vicina Gr. fide Grove 1937]	Wehmeyer (1933)
2.3.1.	D. citri Wolf, Punith & Holl.	
	= Phomopsis citri Fawc.	Punithalingam & Holliday (1973)

1.1.	D. coneglanensis Sacc. & Speg. = Phomopsis coneglanensis (Sacc.) Trav.	Grove (1937)
2.3.1.	D. conjuncta (Fr.) Fckl. = Phomopsis decedens Wehm.	Wehmeyer (1933)
2.2.2.	D. conorum (Desm.) Niessl = Phomopsis occulata (Sacc.) Trav.	Wehmeyer (1933)
2.2.1.	D. controversa (Desm.) Nits. = Phomopsis controversa (Sacc.) Trav.	Wehmeyer (1933)
1.1.	D. corni Fckl. = Phomopsis corni (Sacc.) Trav.	Grove (1937)
2.2.2.	D. coronillae Sacc. = Phomopsis coronillae (West.) Bub.	Wehmeyer (1933)
1.1.	D. crassicolis Nits. = Phomopsis corni (Sacc.) Trav.	Wehmeyer (1933)
	D. crataegi (Curr.) Nits. in litt. ad Fckl. = Phomopsis crataegicola Petr.	Wehmeyer (1933)
2.2.1.	D. crustosa Sacc. & Roum. = Phomopsis crustosa (Sacc., Bomm. & Rouss.) Trav.	Wehmeyer (1933)
1.1.	D. cryptica Nits. = Phomopsis cryptica (Sacc.) Höhn.	Wehmeyer (1933), Grove (1937)
2.2.1.	D. culta Sacc. & Speg. = Phomopsis jasmini (Cke.) Trav.	Wehmeyer (1933)
2.3.1.	D. decedens (Fr.) Fckl. = Phomopsis sp.	Wehmeyer (1927)
2.2.1.	D. decorticans (Lib.) Sacc. & Roum. = Phomopsis padina (Sacc. & Roum.) Died.	Wehmeyer (1933)
2.2.2.	D. delitescens Bomm., Rouss., & Sacc. = Phomopsis liriodendri Gr.	Wehmeyer (1933)
2.2.1.	D. demissa Sacc. = Phomopsis demissa (Sacc.) Trav.	Wehmeyer (1933)
1.1	[?] D. desmazieri Niessl 1.1. = Phomopsis denigrata (Desm.) Trav. 1.1. = Phomopsis desmazieri Gr. var. phlomidis Gr.	Wehmeyer (1933), Grove (1937)
2.2.2.	D. detrusa (Fr.) Fckl. = Phomopsis detrusa (Sacc.) Died	Wehmeyer (1933)
1.1.	D. discors Sacc. [D. maculosa Sacc. = D. rumicis Plowr. fide Grove 1937] = Phomopsis durandiana (Sacc. & Roum.) Died	Wehmeyer (1933)
1.1	D. discors f. polygoni Gr. = Phomopsis polygonorum Gr.	Grove (1937)
2.1.	D. dulcamarae Nits. [≡D. sarothamni (Auersw.) Nits. var. dulcamarae fide Wehmeyer 1933] = Phomopsis dulcamarae (Sacc.) Trav.	Grove (1937)
1.1.	D. epilobii Cke. = Phomopsis epilobii Gr.	Grove (1937)
2.2.2.	D. eres Nits. = Phomopsis buxi (Desm.) Höhn. = Phomopsis oblonga Trav. = Phomopsis occulta Trav.	Wehmeyer (1933), Grove (1937)
2.2.2.	D. euphorbiae Cke. = Phomopsis euphorbiae (Sacc.) Trav.	Wehmeyer (1933)
2.2.1.	D. fibrosa (Pers.) Fckl. = Phomopsis fibrosa (Sacc.) Höhn.	Wehmeyer (1933)
2.2.1.	D. fuchsiae Petr. = Phomopsis sp.	Wehmeyer (1933)
1.1.	D. gloriosa Sacc. & Speg. = Phomopsis gloriosa (Sacc.) Trav.	Wehmeyer (1933)
1.1.	D. importata Nits. = Phomopsis importata (Sacc.) Died.	Wehmeyer (1933)
2.3.1.	D. impulsa (Cke. & Pk.) Sacc. = Phomopsis sp.	Wehmeyer (1933)
2.2.1.	D. inaequalis Nits. = Phomopsis inaequalis Trav.	Wehmeyer (1933)

1.1.	D. incarcerata (Berk. & Br.) Nits.	
	= Phomopsis crustosa (Sacc., Bomm., & Rouss.)	
	1.1. = Phomopsis incarcerata (Sacc.) Höhn., Wehmeyer (1933)	
	= Phomopsis stictica (Berk. & Br.) Trav.	Grove (1937)
1.1.	D. incrustans Nits.	
	= Phomopsis cruciferae Gr.	Grove (1937)
	= [?] Phomopsis incrustans (Sacc.) Died.	Wehmeyer (1933)
2.1.	D. inquilina (Wallr.) Nits.	
	= Phomopsis incrustans Trav.	Wehmeyer (1933)
1.1.	D. insigni Fckl.	
	= Phomopsis insignis Trav.	Wehmeyer (1933)
	= Phomopsis mulleri Gr.	
2.1.	D. intermedia Nits.	
	= Phomopsis corni (Sacc.) Trav.	Wehmeyer (1933)
2.2.1.	D. japonica Sacc.	
	= Phomopsis japonica (Sacc.) Trav.	Wehmeyer (1933)
	= Phomopsis striaeformis Gr.	Grove (1937)
2.2.1.	D. juglandia (Fckl.) Nits.	
	= Phomopsis juglandia (Sacc.) Höhn.	Wehmeyer (1933)
2.3.1.	D. kellermanniana Ell. & Ev. var. batatatis (Harter & Field) Wehmeyer	
	= Phomopsis batatae (Ell. & Halst.) Harter & Field	Wehmeyer (1933)
2.3.1.	D. kellermanniana Ell. & Ev. var sojae (Lehman) Wehmeyer	
	= Phomopsis sp.	Wehmeyer (1933)
2.2.1.	D. landeghemiae (West.) Nits.	
	= Phomopsis landeghemiae (Sacc.) Höhn.	Wehmeyer (1933)
2.1.	D. laschii Nits.	
	= Phomopsis ramealis Died.	
	= Phomopsis foveolaris (Fr.) Trav.	Wehmeyer (1933), Grove (1937)
2.3.1.	D. leiphaemia (Fr.) Sacc.	
	= Phomopsis quercinum (Sacc.) Höhn.	Wehmeyer (1933)
2.1.	D. leycesteriae Grove	
	= Phomopsis leycesteriae Gr.	Wehmeyer (1933)
2.2.1.	D. lingulata Nits.	
	= Phomopsis oblonga (Desm.) Höhn.	Wehmeyer (1933)
2.1.	D. lingulata Nits. [D. nucleata Sacc. fide Groves 1937]	
	= Phomopsis lingulata Gr.	Wehmeyer (1933)
1.1.	D. linearis (Nees) Nits.	
	= Phomopsis linearis (Sacc.) Trav.	Wehmeyer (1933), Grove (1937)
1.1.	D. lirella Fckl.	
	= Phomopsis spiraeae Gr.	Grove (1937)
2.3.1	D. lokoyae Funk	
	= Phomopsis lokoyae Hahn	Funk (1968)
1.1.	D. lupini Harkn.	
	= Phomopsis leptostromiformis Bub.	Grove (1937)
2.2.1.	D. maculosa Sacc. & Speg.	
	= Phomopsis durandiana (Sacc. & Roum.) Died.	Wehmeyer (1933)
1.1.	D. macrostalagmia Tassi	
	= Phomopsis escalloniae Gr.	Grove (1937)
2.3.1.	D. medusaea Nits.	
	= Phomopsis cytosporella Penz. & Sacc.	Fisher (1972)
	2.2.2. = Phomopsis diaporthes-macrostomae (Nits.) Trav.	Wehmeyer (1933)
2.3.1.	D. meglaspora Ell.	
	= Phomopsis sp.	Wehmeyer (1927)
1.1.	D. meliloti (Sacc.) Trav.	
	= Phomopsis meliloti Gr.	Grove (1937)
1.1.	D. minuscula Sacc. & Speg.	
	= Phomopsis minuscula Gr.	Grove (1937)

1.1.	D. mori Berl.	
	= Phomopsis moricola (Sacc.) Gr.	Wehmeyer (1933)
1.1.	D. nobilis Sacc. & Speg.	
	= Phomopsis laurella (Sacc.) Trav.	Wehmeyer (1933), Grove (1937)
2.3.1.	D. oncostoma (Duby) Fckl.	
	= Phomopsis petiolorum (Desm.) Grove	Wehmeyer (1933)
1.1.	D. ophites Sacc.	
	= Phomopsis ophites (Sacc.) Trav.	Wehmeyer (1933)
1.1.	D. orobanches Berl.	
	= Phomopsis orobanches Gr.	Grove (1937)
1.1.	D. orthoceras Nits.	
	= Phomopsis achilleae (Sacc.) Höhn.	Wehmeyer (1933), Grove (1937)
2.1.	D. pardolata (Mont.) Nits.	
	= Phomopsis convallariae (West.) Gr.	Wehmeyer (1933), Grove (1937)
	= Phomopsis pardolata Died.	
2.3.1.	D. peckii Sacc.	
	= Phomopsis sp.	Wehmeyer (1927)
1.1.	D. perexigua Sacc.	
	= Phomopsis perexigua (Sacc.) Trav.	Grove (1937)
1.1.	D. perniciosa March.	
	= Phomopsis mali Roberts.	
	= Phomopsis perniciosa Gr.	
	= Phomopsis prunorum (Cke.) Gr.	Wehmeyer (1933), Grove (1937)
2.3.1.	D. phaseolorum (C. & E.) Sacc.	
	= Phomopsis phaseoli Gr.	Wehmeyer (1933)
1.1.	D. protracta Nits.	
	= Phomopsis platanoidis Died.	Grove (1937)
2.2.1.	D. pulla Nits.	
	= Phomopsis sp.	Wehmeyer (1933), Grove (1937)
1.1.	D. pungens Nits.	
	= Phomopsis pungens (Sacc.) Grove	Wehmeyer (1933), Grove (1937)
2.2.2.	D. pustulata Sacc.	
	= Phomopsis pustulata (Sacc.) Died.	Wehmeyer (1933)
2.1.	D. putator Nits.	
	= Phomopsis putator (Sacc.) Höhn.	Wehmeyer (1933)
1.1.	D. resecans Nits.	
	= Phomopsis depressa (Lév.) Trav.	Wehmeyer (1933)
1.1.	D. retecta Fckl. & Nits.	
	= Phomopsis stictica (B. & Br.) Trav.	Wehmeyer (1933)
1.1.	D. revellens Nits.	
	= Phomopsis revellens (Sacc.) Höhn.	Wehmeyer (1933)
2.3.1.	D. rhoina (C. & E.) Ell.	
	= Phomopsis sp.	Wehmeyer (1927)
1.1.	D. rhois Nits.	
	= Phomopsis rhois (Sacc.) Trav.	Wehmeyer (1933)
1.1.	D. ryckholtii (West.) Nits.	
	= Phomopsis ryckholtii (Sacc.) Höhn.	Wehmeyer (1933)
1.1.	D. samaricola Phil. & Plowr.	
	= Phomopsis pterophila (Fckl.) Died.	Wehmeyer (1933)
2.1.	D. sarothamni (Auersw.) Nits.	
	= Phomopsis sarothamni (Sacc.) Höhn.	Wehmeyer (1933), Gremmen (1965)
2.2.1.	D. sarothamni (Auersw.) Nits. var dulcamarae (Nits.) Wehmeyer	
	= Phomopsis dulcamarae (Sacc.) Trav.	Wehmeyer (1933)
1.1.	D. scabra Nits.	
	= Phomopsis radula Gr.	Grove (1937)
	= Phomopsis scabra (Sacc.) Trav.	Wehmeyer (1933)
1.1.	D. scandens Sacc. & Speg.	
	= Cryptosporium tami Gr.	
	= Phomopsis tamicola (Cooke) Trav.	Wehmeyer (1933), Grove (1937)
1.1.	D. scobina Nits.	
	= Phomopsis scobina (Cke.) Höhn.	Wehmeyer (1933)
1.1.	D. semiimmersa Nits.	
	= Phomopsis semiimmersa (Sacc.) Trav.	Wehmeyer (1933)

1.1.	D. seposita Sacc. = Phomopsis seposita (Sacc.) Trav.	Wehmeyer (1933), Grove (1937)
1.1.	D. skimmiae Gr. = Phomopsis skimmiae Gr.	Grove (1937)
1.1.	D. sophorae Sacc. = Phomopsis sophorae (Sacc.) Trav.	Wehmeyer (1933)
1.1.	D. sorbariae Nits. = Phomopsis sorbariae (Sacc.) Höhn.	Wehmeyer (1933)
1.1.	D. sorbicola (Nits.) Höhn. = Phomopsis sorbicola Gr.	Wehmeyer (1933), Grove (1937)
1.1.	D. sordida Nits. = Phomopsis sordidula (Sacc.) Trav.	Wehmeyer (1933)
2.2.1.	D. spiculosa (Alb. & Schw.) Nits. = Phomopsis sambucella (Sacc.) Trav.	Wehmeyer (1933)
2.3.1.	D. stewartii Harr. = Phomopsis stewartii Pk.	Harrison (1935)
1.1.	D. stictostoma (Ell.) Sacc. [≡Cryptosporella sp. fide Wehmeyer 1933] = Phomopsis stictosoma Gr.	Grove (1937)
2.3.1.	D. strumella (Fr.) Fckl. = Phomopsis sp.	Wehmeyer (1927)
2.2.2.	D. syngenesia (Fr.) Fckl. = Phomopsis syngenesia (Brun.) Höhn.	Wehmeyer (1933)
2.2.1.	D. taleola Sacc. = Endogloea taleola (Sacc.) Höhn. (≡Myxosporium taleolum Sacc.)	Wehmeyer (1933), Sutton (1977)
1.1.	D. tamaricina Sacc. & Flag. = Phomopsis tamaricaria Gr.	Grove (1937)
1.1.	D. tenella (Schw.) Star. = Phomopsis ophities (Sacc.) Trav.	Wehmeyer (1933)
2.3.1.	D. tessela (Pers.) Rehm = ? Phomopsis sp.	Wehmeyer (1933)
1.1.	[?] D. therryana Sacc. & Penz. = Phomopsis hellebori (Brun. & Har.) Trav.	Wehmeyer (1933)
	D. tulasnei Nits. = Phomopsis tulasnei (Sacc.) Trav.	Wehmeyer (1933)
2.3.1.	D. vaccinii Shear = Phomopsis vacinii Shear, Stev. & Bain	Wehmeyer (1933), Shaw (1973)
1.1.	D. velata (Pers.) Nits. = Phomopsis velata (Sacc.) Höhn.	Wehmeyer (1933)
2.3.1.	D. vepris (De Lacr.) Fckl. [≡Apioporthe vepris (DeLacr.) Wehm.] = Phomopsis vepris (Sacc.) Höhn.	Wehmeyer (1933)
2.2.1.	[?] D. veronicae Rehm. = Phomopsis veronicae-speciosae Died.	Wehmeyer (1933)
1.1.	D. verrucella (Fr.) Star. = Phomopsis alnea (Sacc.) Höhn.	Wehmeyer (1933)
	D. vexans Gratz. = Phomopsis vexans (Sacc. & Syd.) Hart.	
1.1.	D. vincae (Cke.) Sacc. [D. eumorpha Maire fide Grove 1937] = Phomopsis lirella Gr.	
1.1.	D. viridarii Sacc. = Phomopsis prunorum (Cke.) Grove	Wehmeyer (1933), Grove (1937)
1.1.	D. viticola Nits. = Phomopsis viticola Sacc.	Grove (1937)
	D. woodii Punith. = Phomopsis leptostromiformis (Kühn) Bubák	Punithalingam & Gibson (1975)
2.3.1.	Diaporthopsis nigrella Fabre. = Phomopsis eryngiicola Trav.	Wehmeyer (1975)
2.3.1.	Diatrype ailanthi (Sacc.) Berl. = Cytosporina ailanthi Sacc.	Arx (1974)
	D. disciformis (Hoffm. ex Fr.) Fr. = Libertella disciformis Höhn.	

	D. radiata Ell. = Cytosporina sp.	
	D. stigma (Hoffm. ex Fr.) Fr. = Libertella betulina Desm. = Naemospora aurea Fr.	
	D. virescens (Schw.) Rav. = Libertella sp.	
	Diatrype sp. = Selenosporella sp.	Carmichael, Kendrick & Conners (1979)
2.3.1.	Diatrypella favacea (Fr.) Ces. & de Not. = Libertella favacea Trav.	Croxall (1950)
2.3.1.	D. quercina (Pers. ex Fr.) de Not. ex Cooke. = Libertella quercina (Sacc.) Gr.	Croxall (1950)
	Dichlaena lentisci Mont. & Dur. = Aspergillus sp.	Malloch & Cain (1972)
2.3.1.	Dichotomomyces cejpii (Milko) Scott var. spinosus (Udag.) Mall. & Cain = Polypaecilum insolitum Smith	Malloch & Cain (1971)
2.2.2.	Diplocarpon earliana (Ell. & Ev.) Wolf = "Marssonia fragariae (Lib.) Nannf." = "Marssonia potentillae Magn." = Septogloeum fragariae Höhn.	Shaw (1973), Sivanesan & Gibson (1976)
2.2.2.	D. maculatum (Atk.) Jørstad = Entomosporium mespili (DC. ex Duby) Sacc. [= Entomosporium maculatum Lév.] fide Sivanesan & Gibson (1976)	Stowell & Backus (1966)
2.3.1.	D. rosae Wolf = Actinonema rosae (Lib.) Fr.	Dodge (1931), Shaw (1973), Sivanesan & Gibson (1976)
2.2.1.	D. polygoni Müller = [?] Bostrichonema alpestris Ces.	Müller (1977)
2.3.1.	D. soraueri (Kleb.) Nannf. = Entomosporium maculatum Lév. (=Entomosporium mespili (DC. ex Duby) Sacc.)	Stowell & Backus (1966)
	Diplogelasinospora grovesii Udagawa & Horie = chlamydospores w. aleuric dehiscence	Udagawa & Horie (1972)
	D. princeps Cain = chlamydospores w. aleuric dehiscence	Cain (1961)
2.1.	Diplostephanus sp. = Sterigmatocystis sp.	Ainsworth et al. (1971), Wehmeyer (1975)
1.1.	Dipodascus sp. = [?] Trichosporon sp.	Tubaki (1958)
2.3.1.	Discohainesia oenotherae (Cooke & Ellis) Nannfeldt = Hainesia rhoina (Sacc.) Ell. & Sacc. = Pilidium concavum (Desm.) Höhn. (≡ Sclerotiopsis concava (Desm.) Shear & Dodge)	Shear & Dodge (1921), Nannfeldt (1932)
2.3.1.	Discostroma canina Brockm. = Sporocadus sp. fide Brockman (1975), see Shoemaker & Müller (1964)	
2.3.1.	D. corticola (Fckl.) Brockm. = Sporocadus sp. fide Brockman (1975)	
2.3.1.	D. massarina (Sacc.) Brockman = Seimatosporium ribis-alpini (Fautrey) Shoem. & Müller	
2.3.1.	D. rosae Brockm. = Seimatosporium rosae Corda	Brockman (1975)
2.3.1.	D. sanguineae Brockm. = Sporocadus fiedleri Rabh.	Brockman (1975)

2.3.1.	D. tosta (B. & Br.) Brockm.	
	= Seimatosporium passerini (Sacc.) Brockm.	Brockman (1975)
	Discoxylaria myrmecophila Lindz. & Wright	
	= Hypocreodendron sanguineum P. Henn.	Ainsworth et al. (1971)
2.3.1.	Drepanopeziza populi-albae (Kleb.) Nannf.	
	= "Marssonia castagnei (Desm. & Mont.) Magn."	Nannfeldt (1932)
2.3.1.	D. populorum (Desm.) Höhn.	
	= "Marssonia populi (Lib.) Magn." (=M. populi-nigrae Kleb.)	Nannfeldt (1932), Gremmen (1965), Shaw (1973)
2.3.1.	D. punctiformis Gremm.	
	= Marssonina sp.	Gremmen (1965)
	D. ribis (Kleb.) Höhn.	
	= Gloeosporidiella ribis (Lib.) Petr.	Klebahn (1918)
	D. salicis (Tul.) Höhn.	
	= Monostichella salicis (Westd.) Arx	Klebahn (1918)
	D. sphaeroides (Fr.) Nannf.	
	= Marssonina salicicola (Bres.) Magn.	Nannfeldt (1931)
	D. tremulae Rimpau	
	= Marssonina brunnea (Ell. & Ev.) Magn.	Klebahn (1918)
	D. triandrae Rimpau	
	= Marssonina kriegeriana (Bres.) Magn.	Rimpau (1961)
2.2.2.	Duplicaria empetri Fckl.	
	= Melasmia empetri Magn.	Korf (1973)
2.3.1	Durandiella lenticellicola Groves	
	= Corniculariella harpographoidea (Dearn.) ex DiCosmo	Groves (1954), DiCosmo (1978)
2.3.1.	D. pseudotsugae Funk	
	= Corniculariella pseudotsugae (White) DiCosmo	Funk (1962), DiCosmo (1978)
2.3.1.	Echinopodospora terrestris Jong & Davis	
	= Chrysosporium sp.	Jong & Davis (1974)
	Edyuillia sp.	
	= Aspergillus sp.	Subramanian (1972)
2.3.1.	Eleutherascus tuberculatus Samson & Luiten	
	= Nodulisporium sp. vel aff. (hyaline)	Samson & Luiten (1975)
2.3.1.	Emericella fruticulosa (Rap. & Fenn.) Mall. & Cain	
	= Aspergillus fruticulosus Rap. & Fenn.	Malloch & Cain (1972)
	E. heterothallica (Kwon, Fenn. & Rap.) Mall. & Cain	
	= Aspergillus heterothallica Kwon, Fenn. & Raper	Malloch & Cain (1972)
	E. julosa (Thom. & Raper) Benjamin	
	= Aspergillus rugulosus Thom. & Raper	Raper & Fennell (1965)
2.3.1.	E. nidulans (Eidam) Vuill.	
	= Aspergillus nidulans (Eidam) Wint. in Rabenh.	Bertoni et al. (1973)
2.3.1	E. nivea Wiley & Simm.	
	= Aspergillus niveus Blochw.	Wiley & Simmons (1973)
2.3.1.	E. parvathecia (Rap. & Fenn.) Mall. & Cain	
	= Aspergillus parvathecius Rap. & Fenn.	Malloch & Cain (1972)
2.3.1.	E. quadrilineata (Thom & Rap.) C.R. Benj.	
	= Aspergillus quadrilineatus Thom. & Rap.	Benjamin (1955)
2.3.1.	E. rugulosa (Thom & Rap.) Benjamin	
	= Aspergillus rugulosus Thom & Raper	Benjamin (1955)
	E. striata (Rai, Rew. & Muk.) Mall. & Cain	
	= Aspergillus striatus Rai, Rew. & Muk.	Malloch & Cain (1972)
2.3.1.	E. unguis Malloch & Cain	
	= Aspergillus unguis (Emile-Weil & Gaudin) Thom & Raper	Malloch & Cain (1972)
	E. variecolor B. & Br. in Berk.	
	= Aspergillus stellatus Curzi	
	E. variicolor Berk. & Br. in Berk. var. astellata (Fenn. & Raper) Benj.	
	= Aspergillus stellatus Curzi	

	E. violacea (Fenn. & Rap.) Mall. & Cain	
	= Aspergillus violaceus Fenn. & Raper	Malloch & Cain (1972)
2.3.1.	Emericellopsis glabra (van Beyma) Backus & Orpurt	
	= Acremonium sp.	Gams (1971)
	E. humicola (Cain) Cain ex Groskl. & Swift	
	= Acremonium sp.	Arx (1970)
2.3.1.	E. microspora Back. & Orp.	
	= Acremonium sp.	Backus & Orpurt (1961)
2.3.1.	E. mirabilis (Malan) Stolk	
	= Acremonium sp.	Gams (1971)
2.3.1.	E. pusilla Mathur & Thirum.	
	= Acremonium sp.	Mathur & Thirumalachar (1960)
2.3.1.	E. robusta van Emden & Gams apud Gams	
	= Acremonium sp.	Gams (1971)
2.3.1.	E. salmosynnemata Groskl. & Swift	
	= Acremonium sp.	Grosklag & Swift (1957)
2.3.1	E. synnematicola Mathur & Thirum.	
	= Stilbella sp.	Mathur & Thirumalachar (1960), Gams (1971)
2.3.1	E. terricola van Beyma	
	= Acremonium sp.	Stolk (1955), Durrell (1959)
2.3.1.	Emmonsiella capsulata Kwon-Chung	
	= Chrysosporium sp.	
	= Histoplasma capsulatum Darling	Carmichael (1962), Kwon-Chung (1972)
2.2.2.	Encoeliopsis laricina (Effl.) Groves	
	= Brunchorstia laricina Effl.	Funk (1969)
1.1.	E. rhododendri (Ces. ex Rehm) Nannf.	
	= Diplodina eurhododendri Voss.	Nannfeldt (1932)
2.3.1	Endomyces geotrichum Butl. & Peters.	
	= Geotrichum candidum Link ex Pers.	Butler & Peterson (1972)
2.3.1	E. magnusi Ludwig	
	= Geotrichum candidum Link ex Pers.	Carmichael (1957)
2.3.1	Endomycopsis lipolytica Wick.	
	= Candida lipolytica (Harr.) Knusel	Wickerham et al. (1970), Kreger-van Rij (1973)
2.3.1	Endothia coccolobii Viz.	
	= Endothiella sp.	Vizioli (1923)
	E. parasitica (Murr.) P.J. & H.W. Anderson	
	= Endothiella gyrosa Sacc.	Anderson & Anderson (1912)
2.3.1.	Ephemeroascus verticillatus van Emden	
	= Verticillium sp.	van Emden (1973)
2.3.1.	Epichloë typhina (Pers. ex Fr.) Tul.	
	= Sphacelia typhina Sacc.	Arx (1970,1974)
	Eriosphaeria aggregata Müll. & Munk	
	= Sporidesmium scutellare B. & Br.	Müller & Munk (1964)
2.2.4.	Erysiphe betae (Vanha) Weltz.	
	= Oidium erysiphoides Fr.	Kapoor (1967)
2.2.4.	E. cichoracearum DC. ex Mérat	
	= Oidium sp.	Kapoor (1967)
2.2.4.	E. cruciferarum Opiz ex Junnel	
	= Oidium sp.	Purnell & Sivanesan (1970)
2.2.4.	E. graminis DC. ex Mérat	
	= Oidium bulbigerum Sacc.	Kapoor (1967)
	= Oidium rubellum Sacc.	
2.2.4.	E. heraclei DC. ex St.-Am.	
	= Oidium sp.	Kapoor (1967)
2.2.4.	E. pisi DC. ex St.-Am.	
	= Oidium sp.	Kapoor (1967)
2.2.4.	E. trifolii Grov.	
	= Oidium orobi Rabenh.	Kapoor (1967)
	Eupenicillium abidjanum Stolk.	
	= Penicillium abidjanum Stolk	
2.3.1.	E. alutaceum Scott	
	= Penicillium alutaceum Scott	Udagawa & Awao (1969), Udagawa, Furuya & Horie (1973)

2.3.1.	E. anatolicum Stolk = Penicillium anatolicum Stolk	Stolk (1968)
2.3.1.	Eupenicillium arvense Udagawa & Yokoyama apud Udagawa & Horie = Penicillium arvense Udagawa & Yokoyama apud Udagawa & Horie	Udagawa & Horie (1974)
2.3.1.	E. baarnense (Beyma) Stolk & Scott = Penicillium baarnense Beyma	Stolk & Scott (1967), Godeas (1975)
2.3.1.	E. brefeldianum (Dodge) Stolk & Scott = Penicillium brefeldianum Dodge	Stolk & Scott (1967), Bertoni et al. (1973)
2.3.1.	E. caperatum Udag. & Hor. = Penicillium caperatum Udag. & Hor.	Udagawa & Horie (1973)
2.3.1.	E. catenatum Scott = Penicillium catenatum Scott	Scott (1968)
2.3.1.	E. cinnamopurpureum Scott & Stolk = Penicillium cinnamopurpureum Abe ex Udag.	Scott & Stolk (1967)
2.3.1.	E. crustaceum Ludwig = Penicillium kewense G. Smith	Stolk & Scott (1967)
2.3.1.	E. egyptiacum (Beyma) Stolk & Scott = Penicillium egyptiacum Beyma	Stolk & Scott (1967)
2.3.1.	E. ehrlichii (Kleb.) Stolk & Scott = Penicillium ehrlichii Kleb.	Stolk & Scott (1967)
2.3.1	E. erubescens Scott = Penicillium erubescens Scott	Scott (1968), Udagawa & Furuya & Horie (1973)
	E. fractum Udag. = Penicillium fractum Udag.	
2.3.1.	E. gracilentum Udag. & Hor. = Penicillium gracilentum Udag. & Hor.	Udagawa & Horie (1973)
2.3.1.	E. hirayamae Scott & Stolk = Penicillium hirayamae Udag.	Scott & Stolk (1967)
	E. idahoense Paden = Penicillium idahoense Paden	
	E. inusitatum Scott = Penicillium inusitatum Scott	
2.3.1.	E. javanicum (Beyma) Stolk & Scott = Penicillium javanicum (Shear) Stolk & Scott	Stolk & Scott (1967,1968), Godeas (1975)
	E. katangense Stolk = Penicillium katangense Stolk	
2.3.1.	E. lapidosum Scott & Stolk = Penicillium lapidosum Raper & Fenn.	Scott & Stolk (1967)
	E. lassenii Paden = Penicillium lassenii Paden	
2.3.1.	E. levitum (Raper & Fennell) Stolk & Scott = Penicillium levitum Raper & Fennell	Stolk & Scott (1967)
2.3.1.	E. ludwigii Udagawa & Awao = Penicillium ludwigii Udagawa & Awao	Udagawa & Awao (1969), Godeas (1975)
	E. luzoniacum Udagawa & Horie = Penicillium luzoniacum Stolk	Udagawa & Horie (1972)
2.3.1.	E. meloforme Udagawa & Horie = Penicillium meloforme Udagawa & Horie	Udagawa & Horie (1973)
	E. meridianum Scott = Penicillium meridianum Scott	
	E. molle Malloch & Cain = Penicillium sp.	Malloch & Cain (1972)
2.3.1.	E. ochrosalmoneum Scott & Stolk = Penicillium ochrosalmoneum Udagawa	Scott & Stolk (1967)
	E. ornatum Udagawa = Penicillium ornatum Udagawa	
2.3.1.	E. osmophilum Stolk & Veenbass-Rijks = Penicillium osmophilum Stolk & Veenbaas-Rijks	Stolk & Veenbaas-Rijks (1974)

2.3.1.	E. papuanum Udagawa & Horie = Penicillium papuanum Udagawa & Horie	Udagawa & Horie (1973)
2.3.1.	E. parvum (Raper & Fennell) Stolk & Scott = Penicillium parvum (Rap. & Fenn.) Udag.	Stolk & Scott (1967)
2.3.1.	E. pinetorum Stolk = Penicillium pinetorum Christ. & Back.	Udagawa (1970)
	E. reticulisporum Udagawa = Penicillium reticulisporum Udagawa	
2.3.1.	E. rubidurum Udagawa & Horie = Penicillium rubidurum Udag. & Hor.	Udagawa & Horie (1973)
2.3.1.	E. shearii Stolk & Scott = Penicillium shearii Stolk & Scott	Stolk & Scott (1967)
	E. stolkiae Scott = Penicillium stolkiae Scott	
	E. terrenum Scott = Penicillium terrenum Scott	
	E. tularense Paden = Penicillium tularense Paden	
	E. zonatum Hodges & Perry = Penicillium zonatum Hodges & Perry	
	Europhium aureum Robinson & Davidson = Verticicladiella sp.	Robinson-Jeffrey & Davidson (1968)
	E. clavigerum Robinson & Davidson = Verticicladiella sp.	Robinson-Jeffrey & Davidson (1968)
	E. robustum Robinson & Davidson = Verticicladiella sp.	Robinson-Jeffrey & Davidson (1968)
2.3.1.	E. trinacriforme Parker = Leptographium sp.	Parker (1957)
2.3.1.	Eurotium amstelodami Mangin = Aspergillus amstelodami (Mangin) Thom & Church	Thom & Raper (1945)
2.3.1.	E. carynoyi (Thom & Raper) C.R. Benj. = Aspergillus carnoyi Biourge, Thom & Raper	Benjamin (1955)
2.3.1.	E. cristatum (Raper & Fennell) Mall. & Cain = Aspergillus cristatus Raper & Fenn.	Malloch & Cain (1972)
2.3.1.	E. chevalieri Mangin = Aspergillus chevalieri (Mangin) Thom & Church	Thom & Raper (1945)
2.3.1.	E. chevalieri Mangin var. intermedium (Thom & Raper) Malloch & Cain = Aspergillus chevalieri (Mangin) Thom & Church var. intermedius Thom & Raper	Thom & Raper (1945)
2.3.1	E. echinulatum Delacroix = Aspergillus echinulatus (Delacr.) Thom & Church	Benjamin (1955)
	E. halophilicus Christ., Papav. & Benj. = Aspergillus halophilicus Christ., Papav. & Benj.	
	E. herbariorum (Wiggers) Link ex Fr. = Aspergillus minor (Mangin) Thom & Raper	de Bary (1854)
	E. heterocaryoticus Christ., Lopez & Benj. = Aspergillus heterocaryoticus Christ., Lopez & Benj.	
2.3.1.	E. montevidense (Talice & MacKinn.) Mall. & Cain = Aspergillus montevidense Talice & MacK.	Malloch & Cain (1972)
2.3.1.	E. niveoglaucum (Thom & Raper) Mall. & Cain = Aspergillus niveoglaucus Thom & Raper	Malloch & Cain (1972)
2.3.1	E. pseudoglaucum (Blóchwitz) Malloch = Aspergillus pseudoglaucum Blochw.	Malloch & Cain (1972)
	E. repens de Bary in de Bary & Woron. = Aspergillus scheelii Bain. & Sart.	

	E. rubrum Konig, Spieck. & Brem. = Aspergillus ruber (Konig, Spieck. & Brem.) Thom & Church = Aspergillus sejunctus Bain. & Sart.	
2.3.1.	E. tonophilum Ohtsuki = Aspergillus tonophilus Ohtsuki	C.B.S. catalogue
2.3.1.	E. umbrosum (Bain. & Sart.) Mall. & Cain = Aspergillus umbrosus Bain. & Sart.	Malloch & Cain (1972)
2.1.	Eutypa acharii Tul. = Cytosporina acharii (Sacc.) Gr.	Grove (1935,1937)
2.1.	E. flavovirens (Hoffm. ex Fr.) Fr. = Cytosporina flavovirens (Sacc.) Gr.	Grove (1935,1937)
2.1.	E. lata (Pers. ex Fr.) Tul. = Cytosporina lata Höhn.	Grove (1935,1937)
1.1.	E. milliaria (Fr. ex Fr.) Sacc. = Cytosporina milliaria Sacc.	Grove (1935,1937)
2.1.	E. rhodi (Nits.) Fckl. = Cytosporina rhodi Höhn.	Grove (1935,1937)
1.1.	Eutypella brunaudiana Sacc. = Cytospora ribis Ehreb.	Grove (1937)
1.1	E. cerviculata (Fr.) Sacc. = Cytosporina cerviculata Sacc.	Shaw (1973)
	E. glomeraria (Berk.) Berl. = Cytosporina sp.	
	E. parasitica Dav. & Lor. = Libertella sp.	Davidson & Lorenz (1938), Johnson & Kuntz (1978)
1.1	E. prunastri (Pers. ex Fr.) Sacc. = Cytospora prunorum Sacc. & Syd.	Grove (1937)
1.1	E. sorbi (Alb. & Schw.) Sacc. = Cytospora rubescens Fr.	Grove (1937), Shaw (1973)
1.1	E. stellulata (Fr.) Sacc. = [?] Cytosporina stellulata Sacc.	Grove (1937)
2.3.1.	Farrowia longicollea (Krzem. & Badura) D. Hawksw. = Botryotrichum sp.	Hawksworth (1975)
2.3.1.	F. malaysiensis D. Hawksw. = Botryotrichum sp.	Hawksworth (1975)
2.3.1.	F. seminuda (L. Ames) D. Hawksw. = Botryotrichum vel aff.	Hawksworth (1975)
2.3.1.	Fennellia flavipes Wiley & Simmons = Aspergillus flavipes (Bainer & Sartory) Thom & Church	Wiley & Simmons (1973)
2.3.1	Fragosphaeria purpurea Shear = Sporothrix sp.	Shear (1923)
2.3.1	F. reniformis (Sacc. & Therry) Mall. & Cain = Sporothrix sp.	Fennell (1973)
	Gaeumannomyces graminis (Sacc.) Arx & Oliver = [?] Coniosporium rhizophilum (Preuss) Sacc. = [?] Hendersonia graminis McAlp. 2.3.1. = Phialophora sp.	McAlpine (1904), Drechsler (1934), Arx (1974)
2.3.1.	Galactinia cerea (Sow ex Mérat) LeGal = Oedocephalum sp.	Berthet (1964)
2.3.1.	G. echinospora (Karst.) LeGal = Oedocephalum sp.	Berthet (1964)
2.3.1.	G. micropus (Pers. ex Fr.) Svrcek = Oedocephalum sp.	Berthet (1964)
2.3.1.	G. violacea (Pers.) LeGal = Oedocephalum sp.	Berthet (1964)
2.3.1	G. vesiculosa (Bull. ex Fr.) Le Gal = Oedocephalum sp.	Berthet (1964)
	Geopyxis carbonaria (Alb. & Schw. ex Fr.) Sacc. = Hansfordia sp.	Paden (1972), Conway (1975)

2.3.1.	G. majalis Fr.	
	= Hansfordia sp.	Paden (1972), Conway (1975)
2.3.1.	Gibberella acuminata Booth	
	= Fusarium acuminatum Ell. & Ev.	Booth (1971)
2.3.1.	G. avenacea Cooke	
	= Fusarium avenaceum (Cda. ex Fr.) Sacc.	Booth (1971)
2.3.1.	G. baccata (Wallr.) Sacc.	
	= Fusarium lateritium Nees ex Fr.	
	= Fusarium lateritium Nees ex Fr. var. fructigenum (Fr.) Wr.	Booth (1971)
2.3.1.	G. buxi (Fckl.) Winter	
	= Fusarium lateritium Nees ex Fr. var. buxi Booth	Booth (1971)
2.3.1.	G. cyanogena (Desm.) Sacc.	
	= Fusarium sulphureum Schlect.	Booth (1971)
2.3.1.	G. fujikuori (Sawada) Ito apud Ito & Kimura	
	= Fusarium moniliforme Shel.	Booth (1971)
2.3.1.	G. gordonia Booth	
	= Fusarium heterosporum Nees. ex Fr.	
2.3.1.	G. intricans Wollenw.	
	= Fusarium equiseti (Cda.) Sacc.	Booth (1971)
2.3.1.	G. pulicaris (Fr.) Sacc.	
	= Fusarium sambucinum Fckl.	Booth (1971)
2.3.1.	G. stilboides Gordon ex Booth	
	= Fusarium stilboides Wollenw.	Booth (1971)
2.3.1.	G. xylariodes Heim & Saccas	
	= Fusarium xylariodes Steyaert	Booth (1971)
2.3.1.	G. zeae (Schw.) Petch.	
	= Fusarium graminarum Schwabe	Booth (1971)
	Gibberella sp.	
	= Stagonostroma sp.	Ainsworth et al. (1971)
	Gloeotinia temulenta (Prill. & Delacr.) Wils.	
	= Endoconidium temulentum Prill. & Delacr.	Nag Raj & Kendrick (1975)
	Glomerella cincta (Stonem.) Spau. & Sch.	
	= Colletotrichum cinctum (B. & C.) Ston.	C.B.S. catalogue, Jenkins (1931)
	G. cingulata (Stonem.) Spau. & Sch.	
	2.3.1. = Colletotrichum fructigenum (Berk.) Vassil.	Arx (1970), Shaw (1973)
	2.3.1. = Colletotrichum gloeosporioides (Penz.) Sacc.	Mordue (1971)
	G. fructigena (Clint.) Sacc.	
	= Colletotrichum fructigenum (Berk.) Vassil.	Shaw (1973)
	G. fusarioides Edj.	
	= Colletotrichum fusarioides (Ell. & Kellerm.) O'Gara in Dearn.	Shaw (1973)
2.3.1.	G. glycines (Horie) Lehman & Wolf	
	= Colletotrichum destructiorum O'Gara	Wolf & Lehman (1920), Tiffany & Gilman (1954)
2.2.1.	G. gossypii Edgerton	
	= Colletotrichum gossypii Southworth	Edgerton (1909)
2.2.3.	G. graminicola Politis	
	= Colletotrichum graminicola (Ces.) Wilson	Politis (1975)
2.3.1.	G. lagernarium (Pass.) Stevens	
	= Colletotrichum lagenarium (Pass.) Ell. & Hals.	
	= Colletotrichum orbiculare (B. & M.) Arx	Stevens (1931)
1.1.	G. lindemuthiana Shear	
	= Colletotrichum lindemuthianum (Sacc. & Magn.) Bri. & Cav.	Grove (1973), Tehon (1937)
2.3.1.	G. nephrolepis Faris	
	= Colletotrichum sp.	Faris (1923)
	G. phacidiomorpha (Ces.) Petr.	
	= Colletotrichum rhodocyclum (Mont.) Pet.	C.B.S. catalogue

1.1.	G. rufo-maculans Spaulding & Schr.	
	= Colletotrichum sp.	Grove (1935)
2.3.1.	G. tucumanensis (Speg.) Arx. & Müller	
	= Colletotrichum falcatum Went.	Mordue (1967), Arx (1970)
	= Colletotrichum graminicola (Ces.) Wilson	
	Gnomonia caryae Wolf	
	= Cylindrosporella caryae (Peck) Petrak	Wolf (1913)
	G. comari Karsten	
	= Zythia fragariae Laibach	
2.3.1.	G. errabunda (Rob.) Auersw.	
	= Discula sp.	Arx (1970)
	G. fimbriata Fckl.	
	= Cylindrosporella carpini (Lib.) Höhn.	
	G. fructicola (Arnaud) Fall	
	= Zythia fragariae Laibach	Fall (1951)
2.3.1.	G. leptostyla (Fr.) Ces. & de Not.	
	= "Marssonia juglandis (Sacc.) Magn."	Fayret (1975)
	G. manihotis Punith	
	= [?] Sporonema sp.	
	G. padi (Lib.) Kleb.	
	= Cylindrosporella padi (DC.) v. Arx	
	G. venta Kleb.	
	= Discula sp.	Grove (1937)
	Gnomonia sp.	
	= Sesquicillium sp.	Carmichael, Kendrick & Conners (1979)
2.1.	Gnomoniella tubiformis (Tode ex Fr.) Sacc.	
	= Colletotrichum sp.	
	= Cylindrosporella sp.	
	= Leptothryrium alneum Sacc.	Shaw (1973)
2.2.2.	Godronia andromedae P. Henn.	
	= Septomyxa andromedae P. Henn.	Groves (1965)
2.2.2.	G. callunigera (Karst.) Karst.	
	= Topospora sp.	Groves (1965)
2.3.1.	G. cassandrae Peck	
	= Fusicoccum putrefaciens Shear	Groves (1965)
2.3.1.	G. cassandrae Peck. f. callunae Groves	
	= Sporonema obturatum (Fr.) Sacc.	Groves (1965)
2.2.4.	G. confertus (Hone) Groves	
	= unnamed coelomycete	Groves (1965)
2.3.1.	G. davidsonii Cash	
	= unnamed coelomycete	Groves (1965)
2.3.1.	G. diervillae Groves	
	= unnamed coelomycete	Groves (1965)
2.3.1.	G. fuliginosa (Fr.) Seaver	
	= Topospora proboscidea (Fr.) Fr.	Groves (1965)
2.3.1	G. grossulariae Groves	
	= Topospora vel aff.	Groves (1965)
2.2.2.	G. menziesiae Groves	
	= unnamed coelomycete	Groves (1965)
2.2.2.	G. muhlenbeckii Moug. & Lév.	
	= [?] Phlyctaena rhizophila Syd.	Groves (1965)
2.3.1.	G. multispora Groves	
	= unnamed coelomycete	Groves (1965)
2.2.2.	G. rhois Groves	
	= unnamed coelomycete	Groves (1965)
2.2.2.	G. ribis (Fries) Seaver	
	= Fuckelia ribis Bon.	Groves (1965)
2.2.2.	G. spiraeae (Rehm) Seaver	
	= unnamed coelomycete	Groves (1965)
2.2.2.	G. symphoricarpi Groves	
	= unnamed coelomycete	Groves (1965)
2.3.1.	G. turbinata (Schw.) Farlow in Thaxter	
	= Topospora vel aff.	Groves (1965)

2.2.2.	G. uberiformis Groves	
	= Topospora uberiformis (Fr.) Fr.	Groves (1965)
2.2.2.	G. urceolata (Ellis) Höhn.	
	= Chondropodiella clethrincola (Ellis) Höhn.	Groves (1965)
2.2.2.	G. urceoliformis (Karst.) Karst.	
	= unnamed coelomycete	Groves (1965)
2.2.2	G. urceolus (Schmidt ex Fr.) Karst.	
	= unnamed coelomycete	Groves (1965)
2.2.2.	G. viburni (Fckl.) Rehm (sub Godronia fuckeliana Groves)	
	= Dothichiza viburni Karst.	Groves (1965)
2.3.1.	Godroniopsis nemopanthis Groves	
	= "Micropera stellatum (Ellis) Jacz."	Groves (1965)
2.3.1.	Graphostroma platystoma (Schw.) Piroz.	
	= Nodulisporium sp.	Pirozynski (1974)
2.3.1.	Griphosphaeria corticola (Fckl.) Höhn.	
	= Seimatosporium sp. (fide Arx 1974)	
	G. nivalis (Schaff.) Müller & Arx	
	= Fusarium nivale (Fr.) Ces.	
2.3.1.	Griphosphaerioma kansensis (Ell. & Ev.) Shoem.	
	= Labridella cornu-cervae Brenckle	Shoemaker (1963)
	Gymnoascella sp.	
	= Malbranchea sp.	Carmichael, Kendrick & Conners (1979)
	Gymnoascoideus sp.	
	= Malbranchea sp.	Carmichael, Kendrick & Conners (1979)
	Gymnoascus sp.	
	= Chrysosporium sp.	Arx (1974)
2.3.1.	Gymnoeurotium athecium (Rap. & Fenn.) Mall. & Cain	
	= Aspergillus athecius Raper & Fennell	Malloch & Cain (1972)
	Habrostictis sp.	
	= Cryptosporiopsis sp.	Korf (1973)
	Halosphaeria cucullata (Kohlm.) Kohlm.	
	= [?] Periconia prolifica Anastasiou	Kohlmeyer (1972,1978)
2.3.1.	H. mediosetigera Cribb. & Cribb.	
	= Trichocladium achrasporum (Meyers & Moore) Dixon ex Shearer & Crane	Shearer & Crane (1977)
2.3.1.	Hamigera avellanea (Thom & Turesson) Stolk & Samson	
	= Penicillium avellaneum Thom & Tur.	Stolk & Samson (1971), Fennell (1973)
2.3.1.	H. striata Stolk & Samson	
	= Penicillium striatum Raper & Fenn.	Stolk & Samson (1971)
2.3.1.	Hanseniaspora sp., Kreger-vanRij	
	= Kloeckera sp.	Kreger-vanRij (1973)
2.1.	Hansensula sp.	
	= Candida sp.	Tubaki (1958), Wickerham, Kurtzman & Herman (1970)
2.3.1.	Hapsidospora irregularis Mall. & Cain	
	= Acremonium sp.	Malloch & Cain (1970), Gams (1971)
2.3.1.	Heleococcum japonense Tub.	
	= Acremonium sp.	
2.2.2.	Helminthosphaeria clavariarum (Tul.) Fckl.	
	= Diplococcium sp.	Bisby (1938), Sutton (1973a)
2.3.1.	"Helotium populinum Fckl."	
	= Cylindrocolla vel aff.	Berthet (1964)
2.3.1.	"H. resinicolum Baranyay & Funk"	
	= Stilbella sp.	Baranyay & Funk (1969)
2.3.1	Hemicarpenteles acanthosporus Udagawa & Takada	
	= Aspergillus acanthosporus Udag. & Tak.	Malloch & Cain (1972)

2.3.1.	H. paradoxus Sarbhoy & Elphick	
	= Aspergillus paradoxus Fenn. & Raper	Ainsworth (1971)
2.2.2.	Hercospora tiliae Fr.	
	= Rabenhorstia tiliae Fr.	Shear (1937), Müller & Arx (1973)
2.2.1.	Heterosphaeria linariae (Rabenh.) Rehm	
	= Heteropatella lacera Fckl.	Grove (1937), Wehmeyer (1937)
2.2.2.	H. patella Bon.	
	= Heteropatella bonordenii Lind.	Grove (1937)
2.2.1.	Higginsia hiemalis (Higgins) Nannfeldt	
	= Phloeosporella sp.	
	= Septocyta sp.	Nannfeldt (1932), Petrak (1939), Korf (1973)
2.2.1.	H. jaapii (Rehm) Nannf.	
	= Hainesia feurichii Bub.	Nannfeldt (1932)
2.2.1.	H. kerriae (Stew.) Nannf.	
	= "Cylindrosporium" kerriae Stew.	Nannfeldt (1932)
2.2.1.	H. lutescens (Higg.) Nannf.	
	= "Cylindrosporium" lutescens Higg.	Nannfeldt (1932)
2.2.1.	H. prunophorae (Higg.) Nannf.	
	= "Cylindrosporium" prunophorae Higg.	Nannfeldt (1932)
	Holwaya leptosperma (Peck) Durand.	
	= Crinula caliciiformis Fr.	Sutton (1973a)
2.2.2.	Hyaloscypha cladii Nag Raj & Kendrick	
	= Chaetochalara cladii Sutton & Piroz.	Nag Raj & Kendrick (1975)
	H. dematiicola (Berk. & Br.) Nannf.	
	= Haplographium delicatum Berk. & Br.	Hughes (1953)
2.3.1.	Hymenopleella sollmannii Shoem. & Müller	
	= Seiridium vel aff.	Shoemaker & Müller (1965)
2.3.1.	Hymenoscyphus caudatus (Karst.) Dennis	
	= Idriella sp.	Kimbrough (1975)
2.3.1.	H. varicosporoides Tubaki	
	= Varicosporium sp.	Tubaki (1966), Kimbrough (1975)
2.3.1.	Hypocrea atrogelatinosa Dingley	
	= Trichoderma viride Pers. ex Fr.	Dingley (1957)
2.3.1.	H. aureo-viridis Plowr. & Cooke apud Phill. & Plowr.	
	= Trichoderma sp.	Dingley (1951)
2.3.1.	H. citrina (Fr.) Fr.	
	= Acremonium sp.	Canham (1969)
2.3.1.	H. coprosma Dingley	
	= Trichoderma viride Pers. ex Fr.	Dingley (1957)
2.3.1.	H. gelatinosa (Tode ex Fr.) Fr.	
	= [?] Gliocladium sp.	
	= [?] Penicillium sp.	Webster (1964)
2.3.1.	H. hunua Dingley	
	= Trichoderma viride Pers. ex Fr.	Dingley (1957)
2.3.1.	H. lactea (Fr. ex Fr.) Fr.	
	= Acremonium sp.	
	= Trichoderma album Preuss	
	= Trichoderma sporulosum (Link) Hughes	Dingley (1957), Gams (1971), Rogerson pers. comm.
2.3.1.	H. pilulifera Webster & Rifai	
	= Trichoderma piluliferum Webs. & Rifai	Webster & Rifai (1968)
2.3.1.	H. psychrophila Müller, Aebi & Webster	
	= Gliocladium vel aff.	Müller, Aebi & Webster (1972)
2.3.1.	H. rufa (Pers. ex Fr.) Fr.	
	= Trichoderma viride Pers. ex Fr.	Dingley (1957)
2.3.1.	H. schweinitzii (Fr.) Schw.	
	= Trichoderma viride Pers. ex Fr.	Dingley (1957)
2.3.1.	H. semiorbis Berk.	
	= Trichoderma viride Pers. ex Fr.	Dingley (1957)
	H. splendens Phil. & Plowr.	
	= Fusarium splendens Mats. & Kobay.	

2.3.1.	H. sulfurea (Schw.) Fr.	
	= Acremonium sp.	Dingley (1957)
2.3.1.	H. tawa Dingley	
	= Trichoderma viride Pers. ex Fr.	Dingley (1957)
2.3.1.	H. vinosa Cke.	
	= Trichoderma viride Pers. ex Fr.	Dingley (1957)
	Hypocrea sp.	
	= Trichoderma sp.	Webster (1964)
2.2.2.	Hypocrella aleyrodes Sawada	
	= Aschersonia aleyrodes Sawada	Kobayashi (1973)
2.2.2.	H. cretacea Höhn.	
	= Aschersonia sp.	Seaver (1920), Ainsworth et al. (1971)
2.2.2.	H. epiphylla (Mass.) Sacc.	
	= Aschersonia cubensis Berk. & Curt.	Kobayashi (1973)
2.2.2.	H. javanica (Penz. & Sacc.) Petch	
	= Aschersonia coffeae Henn.	Kobayashi (1973)
2.2.2.	H. phyllogena (Mont.) Petch	
	= Aschersonia basieystis Berk. & Curt.	Kobayashi (1973)
2.2.2.	H. reineckiana Henn.	
	= Aschersonia marginata Ell. & Ev.	Kobayashi (1973)
2.2.2.	H. turbinata (Berk.) Seaver	
	= Aschersonia tubinata Thax.	Seaver (1920)
2.3.1	Hypocreopsis lichenoides (Tode ex Fr.) Seaver	
	= Stromatocrea cerebriforme Cooke	Cauchon & Ouellette (1964)
2.2.2.	Hypoderma commune Duby	
	= Leptothyrium vulgare Sacc.	Grove (1937)
2.2.2.	H. hederae de Not.	
	= Leptothyrium hederae Starb.	Grove (1937)
2.2.2.	H. hedgcocki Dearness	
	= Leptostroma sp.	Dearness (1926)
2.2.2.	H. lethale Dearness	
	= Gloeosporium sp.	Dearness (1926)
2.2.2.	H. scirpinum DC.	
	= Leptothyrium scirpinum Bub. & Kab.	Grove (1937)
1.1.	H. virgultorum DC.	
	= Leptostroma virgultorum Sacc.	Grove (1937)
	Hypodermella laricis Tubeuf.	
	= Leptothyrella laricis Dearn.	Korf (1973), Shaw (1973)
	Hypomyces albidus Rehm	
	= Sibirina sp.	Arnold (1971), Samuels (1976)
2.2.1.	H. asterophorus Tul.	
	= [?] Polyscytalum fungorum Sacc.	Petch (1938), Nag Raj & Kendrick (1975)
2.3.1.	H. aurantius (Pers. ex S.F. Gray) Tul.	
	= Cladobotryum varium Nees per Duby	Gams & Hoozemans (1970), Arnold (1971)
2.3.1.	H. aureo-nitens L.R. Tulasne & C. Tulasne	
	= Gliocladium penicillioides Cda.	Samuels (1976)
	H. australis (Mont.) Tul.	
	= Cladobotryum sp.	
	= Trichothecium vel aff.	Arnold (1971)
	H. batavus G. Arnold	
	= Verticillium sp.	
2.3.1.	H. berkeleyanus Plowr. & Cooke	
	= [?] Verticillium berkeleyanum Karst.	Samuels (1976)
2.2.1.	H. broomeanus Tul.	
	= Gliocladium strictum Petch	
	= Moeszia sp.	Petch (1938), Arnold (1971)
2.2.2.	H. cervinigenus Rogerson & Simms	
	= Mycogone cervina Ditm. ex Sacc.	
	= Verticillium sp.	Rogerson & Simms (1971), Rogerson pers. comm.
	H. chromaticus Berk. & Broome	
	= Cladobotryum sp.	
	= Trichothecium vel aff.	Arnold (1971)

2.2.2.	H. chrysospermum (Bull.) Tul.	
	= Sepedonium chrysospermum Link ex Fr.	
	= Verticillium sp.	Seaver (1910), Damon (1952)
	H. chrysostomus Berk. & Br.	
	= Gliocladium sp.	
	= Moeszia sp.	Arnold (1971)
	H. dactylarioides G. Arnold	
	= Cladobotryum sp.	
	= Dactylaria sp.	
	= Dactylium sp.	Arnold (1971)
	H. javanicus Höhn.	
	= Cladobotryum sp.	
	= Trichothecium vel aff.	Arnold (1971)
	H. lactifluorum (Schw. ex Fr.) Tul.	
	= Verticillium sp.	Arnold (1971)
	H. macrosporus Seaver	
	= Verticillium sp.	Arnold (1971)
2.3.1.	H. odoratus G. Arnold	
	= Cladobotryum mycophilum (Oudem) Gams & Hoozem.	Gams & Hoozemans (1970), Arnold (1971)
2.2.1.	H. ochraceus (Pers.) Tul.	
	= Verticillium agaricinum Cda.	
	= Blastotrichum puccinioides Preuss	Petch (1938)
	H. petchii G. Arnold	
	= Verticillium sp.	Arnold (1971)
	H. polyporinus Peck	
	= Gliocladium sp.	
	= Moeszia sp.	
	= Trichothecium vel aff.	Arnold (1971)
2.3.1.	H. rosellus (Alb. & Schw. per Fr.) Tul.	
	= Cladobotryum dendroides (Bull. ex Mérat) Gams & Hoozem.	Gams & Hoozemans (1970), Arnold (1971)
	H. semitranslucens G. Arnold	
	= Sibirina sp.	Arnold (1971)
	H. subiculosus (Berk. & Curt.) Höhn.	
	= Cladobotryum sp.	
	= Trichothecium vel aff.	Arnold (1971)
	H. sulphureus Syd.	
	= Cladobotryum sp.	
	= Trichothecium vel aff.	Arnold (1971)
	H. tegillum Berk. & Curt.	
	= Cladobotryum sp.	
	= Dactylaria sp.	
	= Dactylium sp.	Arnold (1971)
	H. tremellicola (Ellis & Ev.) Rogerson	
	= Verticillium sp.	Samuels (1976)
	H. trichoderma (Hoffm. ex Fr.) Sacc.	
	= Cladobotryum sp.	
	= Trichothecium vel aff.	Arnold (1971)
2.3.1.	H. trichothecioides Tubaki	
	= Cladobotryum sp.	
	= Trichothecium sp.	Rifai & Cooke (1966), Gams & Hoozemans (1970), Arnold (1971)
	H. tulasneanus Plowr.	
	= Sepedonium tulasneanum Plowr.	Plowright (1882), Damon (1852)
1.1.	Hypomyces spp.	
	= Stephanoma spp.	Barron (1968)
1.1.	Hyponectria buxi Sacc.	
	= Macrophoma mirbeli Berl. & Vogl.	Grove (1935)
	Hypoxylon albocinctum Ell. & Ev.	
	= Virgariella sp.	Jong & Rogers (1972)
2.3.1.	H. cohaerens Pers. ex Fr.	
	= Nodulisporium vel aff.	Jong & Rogers (1972)

2.3.1.	H. confluens (Tode ex Fr.) West.	
	= Nodulisporium vel aff.	Chesters & Greenhalgh (1964)
2.3.1.	H. diathrauston Rehm	
	= Nodulisporium vel aff.	Jong & Rogers (1972)
2.3.1.	H. fragiforme (Pers. ex Fr.) Kickx.	
	= Nodulisporium sp.	Jong & Rogers (1972), de Hoog (1974)
2.3.1.	H. fuscum Pers. ex Fr.	
	= Acrostaphylus vel aff.	
	= Virgariella vel aff.	Rogers (1966a)
2.3.1.	H. grenadense J.H. Miller var. macrospora J.H. Miller	
	= Acrostaphylus vel aff.	
	= Virgariella vel aff.	Rogers (1966b)
2.3.1.	H. howeianum Peck	
	= Nodulisporium sp.	Greenhalgh & Chesters (1968)
2.3.1.	H. investiens (Schw.) Curt. var investiens	
	= Nodulisporium vel aff.	Jong & Rogers (1972)
	H. microplacum (B. & C.) J.H. Miller	
	= Nodulisporium vel aff.	Jong & Rogers (1968,1972)
2.3.1.	H. mediterraneum (de Not.) J.H. Miller	
	= Nodulisporium vel aff.	Jong & Rogers (1972)
2.3.1.	H. mediterraneum (de Not.) J.H. Miller var. microspora J.H. Miller	
	= Nodulisporium vel aff.	Jong & Rogers (1972)
2.3.1.	H. multiforme Fr.	
	= Nodulisporium sp.	Jong & Rogers (1972)
2.3.1.	H. nummularium Bull ex Fr.	
	= Nodulisporium vel aff.	Greenhalgh & Chesters (1968)
2.3.1.	H. punctulatum (Berk. & Rav.) Cke.	
	= Xylocladium sp.	Barnett (1957), Jong & Rogers (1972)
	H. pynaerthii Bres.	
	= Virgariella sp.	Jong & Rogers (1972)
2.3.1.	H. rubiginosum Pers. ex Fr.	
	= Virgariella sp.	Greenhalgh & Chesters (1968), Jong & Rogers (1972)
	H. sassafras (Schw. ex Fr.) Curt.	
	= Virgariella sp.	Jong & Rogers (1972)
2.3.1	H. serpens (Pers. ex Fr.) Fr.	
	= Nodulisporium corticioides (Ferr. & Sacc.) Hughes	Chesters & Greenhalgh (1964)
2.3.1.	H. serpens (Pers. ex Fr.) Kickx. var. macrospora J.H. Miller	
	= Nodulisporium vel aff.	Jong & Rogers (1972)
2.3.1.	H. tinctor (Berk.) Cooke	
	= Xylocladium sp.	Jong & Rogers (1972)
2.3.1.	H. truncatum (Schw. ex Fr.) J.H. Miller	
	= Acrostaphylus vel aff.	Jong & Rogers (1972)
2.3.1.	H. vogesiacum Pers. ex Sacc.	
	= Nodulisporium vel aff.	Jong & Rogers (1972)
	Hypoxylon sp.	
	= Triplicaria sp.	Ainsworth (1961)
2.3.1.	Iodophanus carneus (Pers. per Pers.) Korf apud Kimbr. & Korf	
	= Oedocephalum sp.	Kimbrough & Korf (1967), Paden (1972)
2.3.1.	Keratinophyton terreum Randhawa & Sandhu.	
	= Trichophyton vel aff.	Apinis (1968)
2.3.1.	Kernia hippocrepida Malloch & Cain	
	= Scopulariopsis sp.	Malloch & Cain (1970)
	= [?] Graphium sp.	
2.3.1.	K. hyalina Malloch & Cain	
	= Scopulariopsis sp.	Malloch & Cain (1970)
2.3.1.	K. nitida (Sacc.) Nieuw.	
	= Scopulariopsis sp.	

2.3.1.	K. pachypleura Malloch & Cain = Scopulariopsis sp.	Malloch & Cain (1970)
2.3.1.	Khuskia oryzae Hudson = Nigrospora oryzae (B. & Br.) Petch	Hudson (1963)
	Korfiella sp. = Conoplea sp.	de Hoog (1977)
	Lachnellula agassizii (B. & C.) Dennis = [?] Naemospora sp.	Dharne (1965)
	L. arida (Phill.) Dennis = [?] Naemospora sp.	Dharne (1965)
	L. flavovirens (Bres.) Dennis = [?] Naemospora sp.	Dharne (1965)
	L. fuckelii (Bres. apud Rehm) Dharne = [?] Naemospora sp.	Dharne (1965)
	L. fuscosanguinea (Rehm) Dennis = [?] Naemospora sp.	Dharne (1965)
	L. hyalina Dharne = [?] Naemospora sp.	Dharne (1965)
	L. laricis (Cooke) Dharne = [?] Naemospora sp.	Dharne (1965)
	L. minuta Dharne = [?] Naemospora sp.	Dharne (1965)
	L. occidentalis (Hahn & Ayers) Dharne = [?] Naemospora sp.	Dharne (1965)
	L. resinaria (Cooke & Phill.) Rehm = [?] Naemospora sp.	Dharne (1965)
	L. subtilissima (Cooke) Dennis = [?] Naemospora strobii All.	Dharne (1965)
	L. suecica (de Bary ex Fckl.) Nannf. = [?] Naemospora sp.	Dharne (1965)
	L. tuberculata Dharne = [?] Naemospora sp.	Dharne (1965)
	L. willkommii (Hartig) Dennis = [?] Naemospora sp.	Dharne (1965)
	Lasiosphaeria hirsuta (Fr.) Ces. & de Not. = Phialophora sp.	Tubaki (1958)
2.2.1.	Lepteutypa cisticola Ade = Adea canariensis Petrak	Petrak (1929)
2.3.1.	L. cupressi (Nattrass, Booth & Sutton) Swart = Seiridium sp.	Swart (1973)
	L. indica (Punithalingam) Arx = Hyalotiopsis subramanianii Agnih. ex Punith.	Punithalingam (1969), Arx (1974)
2.2.2.	Leptotrochila bartsiae Schüepp = Sporonema sp.	Schüepp (1959)
2.2.2.	L. medicaginis (Fckl.) Schüepp = Sporonema sp.	Schüepp (1959)
2.2.2.	L. pedicularis (Müller & Schüepp) Schüepp = Sporonema sp.	Schüepp (1959)
2.2.2.	L. phyteumatis (Fckl.) Schüepp = Sporonema sp.	Schüepp (1959)
2.2.2.	L. radians (Rob.) Karst., Schüepp = Sporonema sp.	Schüepp (1959)
2.2.2.	L. trifolii-arvensis (Nannf.) Schüepp = Sporonema sp.	Schüepp (1959)
2.2.2.	L. verrucosa (Wallr.) Schüepp = Sporonema sp.	Schüepp (1959)
	Leucostoma leucostoma (Fr.) Togashi = Cytospora leucostoma Sacc.	Grove (1935)
2.3.1.	L. sequoiae Bonar = Cytospora sp.	Bonar (1928)
2.3.1.	Leucothecium emdenii Arx & Samson = Aspergillus sp.	Arx & Samson (1973)

1.1.	Leveillula taurica (L.) Arn.	
	= Oidiopsis taurica (Lév.) Salmon	Mukerji (1968)
	Leveillula sp.	
	= Oidiopsis gossypii (Wakef.) Raych.	Tubaki (1958)
1.1.	Levispora sp.	
	= Acremonium sp.	Tubaki (1958)
	Lilliputia insignis (Winter) Dennis & Wakef.	
	= Gliocladium sp.	Dennis & Wakefield (1946)
	Lilliputia sp.	
	= Phialocephala sp.	Dennis & Wakefield (1946)
1.1.	Lipomyces sp.	
	= Cryptococcus sp.	Tubaki (1958)
2.2.2.	Lophodermium arundinaceum (Schrad.) Chev.	
	= Leptostromella graminicola Gr.	Nannfeldt (1932), Grove (1937)
2.2.2.	L. australe Dearn.	
	= Leptostroma sp.	Dearness (1926)
2.2.2.	L. berberidis (Schleich.) Rehm	
	= Leptothyrium berberidis (Thüm. & Wint.)	Nannfeldt (1932)
2.2.2.	L. cedrinum R. Maire	
	= Labrella cedrina Dur. & Mont.	Nannfeldt (1932)
2.2.1	L. laricinum Fckl.	
	= Leptostroma laricinum Fckl.	Grove (1937)
2.2.2.	L. laricis Dearness	
	= Leptostroma sp.	Dearness (1926)
2.2.1.	L. melaleucum de Not.	
	= Leptothyrium melaleucum Gr.	Grove (1937)
2.2.2.	L. paeoniae Rehm	
	= Leptostroma hysterioides Fr.	Nannfeldt (1932)
2.2.2.	L. pinastri (Fr.) Chev.	
	= Leptostroma pinastri Desm.	Shaw (1973)
2.2.2.	L. robergei Desm.	
	= [?] Leptostromella septorioides Sacc. & Roum.	Nannfeldt (1932)
2.2.2.	L. xylomoides Chev.	
	= Leptostroma crataegi Nannf.	Nannfeldt (1932)
	Lophotrichus sp.	
	= Humicola sp.	Carmichael, Kendrick & Conners (1979)
	Macronodus sp.	
	= Malbranchea sp.	Carmichael, Kendrick & Conners (1979)
2.3.1.	Magnaporthe grisea (Herbert) Barr	
	= Pyricularia grisea (Cke.) Sacc.	Barr (1977), Yaegashi & Udagawa (1978a,b)
2.3.1.	M. salvinii (Catt.) Krause & Webster	
	= Nakataea sigmoidea (Cav.) Hara	Subramanian (1970), Krause & Webster (1972)
	Martininia panamaensis Dumont & Korf	
	= [?] Myrioconium sp. (spermatial)	Dumont & Korf (1970)
	Mazzantia galii Mont.	
	= Placosphaeria galii Sacc.	Grove (1935)
2.2.2.	Melanconis alni Tul.	
	= Melanconium apiocarpum Link	
	= Melanconium sphaeroideum Link	Grove (1937), Wehmeyer (1941)
2.3.1.	M. alni Tul. var. marginalis (Pk.) Wehmeyer	
	= Melanconium sp.	Wehmeyer (1941)
2.3.1.	M. apocrypta Ell.	
	= Melanconium populinum Pk.	Wehmeyer (1941)
	M. carthusiana Tul.	
	= Melanconium juglandinum Kunze apud Ficinua	
	= Melanconium ovatum (Pers.) Link	Grove (1937)
2.3.1.	M. corni Wehmeyer	
	= unnamed coelomycete	Wehmeyer (1940)

2.3.1.	M. decoraensis Ellis	
	= Melanconium sp.	Wehmeyer (1926)
2.2.2.	M. everhartii Ell.	
	= Melanconium ovatum (Pers.) Link	Wehmeyer (1941)
2.2.2.	M. flavo-virens (Otth.) Höhn.	
	= Melanconium sp.	Wehmeyer (1937,1941)
2.3.1	M. juglandis (Ell. & Ev.) Graves	
	= Melanconium microsporum Nees	Graves (1923), Wehmeyer (1940)
2.3.1.	M. juglandis (Ell. & Ev.) Graves var. caryae Wehmeyer	
	= unnamed coelomycete with dimorphic conidia	Wehmeyer (1940)
	M. macrosperma Tul.	
	= Melanconium magnum Berk.	Grove (1935)
	M. occulta (Fckl.) Sacc.	
	= [?] Cytospora occulta Sacc.	Wehmeyer (1941)
2.3.1.	M. ostryae (Dearn.) Wehmeyer	
	= Melanconium sp.	Wehmeyer (1937,1941)
2.2.2.	M. platystroma Wehmeyer	
	= Melanconium sp.	Wehmeyer (1937,1941)
	M. spodiae Tul.	
	= Melanconium sp.	Wehmeyer (1941)
1.1.	= Melanconium stromaticum Corda	Grove (1937)
1.1.	= Myxosporium deplanatum Sacc.	Grove (1937)
2.3.1.	M. stilbostoma (Fr.) Tul.	
	= Melanconium betulinum Schm. & Kunze	
	= Melanconium bicolor Nees	
	= Melanconium zonatum Ell. & Ev. apud Peck	Grove (1937), Wehmeyer (1941), Müller & Arx (1962)
2.3.1.	M. sudans (B. & C.) Wehmeyer	
	= Melanconiopsis inquinans Ell. & Ev.	Wehmeyer (1939)
2.2.2.	M. theobola (Fr.) Sacc.	
	= [?] Cytospora umbrina (Bon.) Sacc.	
	= [?] Stilbospora thelobola Sacc.	Wehmeyer (1941)
	Melanconis sp.	
	= [?] Coryneum sp.	Arx (1974)
2.3.1.	M. xanthostroma (Mont.) Schröt.	
	= Melanconium ramulorum Cda.	
	= Myxosporium carpini Gr.	Wehmeyer (1937)
	Melanochaeta aotearoae (Hughes) Müller, Harr. & Sulmont	
	= Sporoschisma mirabile B. & Br.	Müller, Harr & Sulmont (1969)
	M. hemipsila (B. & Br.) Müll., Harr & Sulm.	
	= Sporoschisma saccardoi Hughes & Mason apud Hughes	Müller, Harr & Sulmont (1969)
2.3.1.	Melanopsamma pomiformis (Pers. ex Fr.) Sacc.	
	= Stachbotrys chartarum (Ehrenb. ex Link) Hughes	Booth (1957)
2.3.1.	Melanopsammella inaequalis (Grove) Höhnel	
	= Gonytrichum caesium Nees & Nees	Höhnel (1919), Ellis (1971)
	Melanospora brevirostrata Moreau	
	= [?] Harzia	Moreau (1945), Tubaki (1958)
2.3.1.	M. damnosa (Sacc.) Lindaw	
	= [?] Harzia vel aff.	
	= [?] Chlamydomyces vel aff.	Mason (1933)
2.3.1.	M. episphaeria Phil. & Plowr.	
	= [?] Acremonium sp.	
	= [?] Paecilomyces sp.	Goos (1956)
	M. fusispora (Petch) Doguet	
	= Paecilomyces vel aff.	Doguet (1955)
	M. mangini Vincens	
	= Paecilomyces sp.	Vincens (1917)
2.3.1.	M. ornata Zukal	
	= [?] Paecilomyces sp.	Furuya & Udagawa (1973)

2.3.1.	M. zamiae Corda	
	= [?] Harzia vel aff.	Mason (1933)
	Melanospora sp.	
	= Proteophiala mattiroliana Cif.	Ciferri (1957)
	Melogramma rubricosum Fckl.	
	= [?] Naemospora microscopica Desm.	Grove (1937)
	Merostictis circinata (Lib.) Défago	
	= Acremonium sp.	Défago (1967)
	Metschnikowia pulcherrima Pitt & Miller	
	= Candida pulcherrima (Lind.) Wind.	Pitt & Miller (1968)
	2.3.1. = M. reukaufii Pitt & Miller	
	= Candida reukaufii (Gruss) Diddens & Lodder	Pitt & Miller (1968)
2.2.2.	Micraspis acicola Darker	
	= Periperidium acicola Darker	Darker (1963)
2.3.1.	Microascus albo-nigrescens (Sopp) Curzi	
	= Scopulariopsis sp.	Barron et al. (1961), Morton & Smith (1963)
2.3.1.	M. cinereus (Emilé-Weil & Gaudin) Curzi	
	= Scopulariopsis cinerea Emilé-Weil & Gaudin	Barron et al. (1961), Morton & Smith (1963)
2.3.1.	M. cirrosus Curzi	
	= Scopulariopsis sp.	Barron et al. (1961)
2.3.1.	M. desmosporus (Lechmere) Curzi	
	= Scopulariopsis paisii (Pollacci) Nannizzi	Barron et al. (1961)
2.3.1.	M. doguetii Moreau	
	= Scopulariopsis sp.	Barron et al. (1961)
2.3.1.	M. giganteus Malloch	
	= Wardomyces sp.	Malloch (1970)
2.3.1.	M. inopinatus Udagawa & Furuya	
	= Wardomycopsis inopinata Udag. & Fur.	Udagawa & Furuya (1978)
2.3.1.	M. longirostris Zukal	
	= Scopulariopsis sp.	Barron et al. (1961), Morton & Smith (1963)
2.3.1.	M. lunasporus Jones	
	= Scopulariopsis lunaspora Jones	Jones (1936)
2.3.1.	M. mangini (Loubière) Curzi	
	= Scopulariopsis candida (Pers.) Loub. (Paecilomyces sp. fide Tubaki)	Morton & Smith (1963)
	M. niger (Sopp) Curzi	
	= Scopulariopsis asperula (Sacc.) Hughes	C.B.S. catalogue
2.3.1.	M. pedrosoi Fuentes & Wolf	
	= Phialophora sp.	Fuentes & Wolf (1956), Subramanian (1971)
2.3.1.	M. pyramidus Barron & Gilman	
	= Scopulariopsis sp.	Barron et al. (1961)
2.3.1.	M. singularis (Sacc.) Malloch & Cain	
	= Wardomycopsis sp.	Udagawa & Furuya (1978)
2.3.1.	M. stysanophorous (Matt.) Barron, Cain & Gilman	
	= Scopulariopsis sp.	Barron et al. (1961)
2.3.1.	M. trigonosporus Emmons & Dodge	
	= Scopulariopsis trigonospora Emmons & Dodge	Emmons & Dodge (1931)
2.3.1.	Microascus sp.	
	= Dermatophora glomerata Viala	Curzi (1935)
2.3.1.	Microascus sp.	
	= Scopulariopsis sp.	Arx (1970)
2.3.1.	Micronectriella cucumeris (Kleb.) Booth	
	= Fusarium tabacinum (Beyma) Gams	Booth (1971)
	M. nivalis (Schaffn.) Booth	
	= Fusarium nivale (Fr.) Ces.	Booth (1971)

2.3.1.	M. stoveri Booth	
	= Fusarium stoveri Booth	Booth (1971)
	Microsphaera platani Howe	
	= Oidium sp.	Sumstine (1941)
2.3.1.	Microthecium ciliatum Udag. & Taka.	
	= [?] Acremonium sp.	
	= [?] Paecilomyces sp.	Udagawa & Takada (1974)
2.3.1.	M. compressum Udagawa & Cain	
	= [?] Acremonium sp.	
	= [?] Paecilomyces sp.	Udagawa & Cain (1969)
2.3.1.	M. levitum Udagawa & Cain	
	= [?] Acremonium sp.	
	= [?] Paecilomyces sp.	Udagawa & Cain (1969)
2.3.1.	M. retisporum Udagawa & Cain	
	= [?] Acremonium sp.	
	= [?] Paecilomyces sp.	Udagawa & Cain (1969)
2.3.1.	Miladina lechithina (Cooke) Svrcek	
	= Actinospora megalospora Ingold	Descals & Webster (1978)
	Mollisia cinerella Sacc.	
	= Phialophora melinii (Nannf.) Conant	LeGal & Mangenot (1961), Schol-Schwarz (1970)
	Mollisia sp.	
	= Anguillospora crassa Ingold	Webster (1961)
	Mollisia sp.	
	= Phialophora sp.	Korf (1973)
2.3.1.	Monascus ruber vanTiegh.	
	= Basipetospora rubra Cole & Kendr.	Cole & Kendrick (1968)
2.3.1.	Monilinia fructicola (Winter) Honey	
	= Monilia sp.	
2.3.1.	M. fructigena (Aderh. & Ruhl.) Honey	
	= Monilia fructigena Pers.	Barron (1968)
	M. gregaria (Dana) Honey	
	= Monilia gregaria Dana	Dana (1921)
2.3.1.	M. laxa (Aderh. & Ruhl.) Honey	
	= Monilia cinerea Bon.	
	= Monilia cinerea Bon. var. mali (Wormald) Harrison	
	= Monilia laxa (Ehrenb. ex Wallr.) Sacc.	Shaw (1973)
2.3.1.	M. ledi (Nawaschin) Whetzel	
	= Monilia sp.	Whetzel (1945)
2.3.1.	Morchella elata Fr.	
	= Costantinella sp.	Paden (1972)
2.3.1.	M. esculenta Pers.	
	= Costantinella sp.	Molliard (1904a,b)
2.3.1.	Mycoarachis inversa Malloch & Cain	
	= Acremonium sp.	Malloch & Cain (1970)
2.3.1.	Mycocitrus aurantius Moeller	
	= Acremonium sp.	Gams (1971)
2.2.2.	Myriosclerotinia sp.	
	= Myrioconium sp. (spermatial state)	Korf (1973)
2.3.1.	Myrmaeciella sp.	
	= Patellina sp.	Rogerson pers. comm.
2.3.1.	Myxotrichum ochraceum (Berk. & Por.) Ber.	
	= Oidiodendron ambiguum (Peyr.) Malan	Sigler & Carmichael (1976)
2.3.1.	M. spinosum Massee & Salmon	
	= Oidiodendron sp.	Sigler & Carmichael (1976)
2.3.1.	Myxotrichum sp.	
	= Malbranchea circinata Sigl. & Carm.	Sigler & Carmichael (1976)
2.3.1.	Myxotrichum sp.	
	= Malbranchea flavoroseus Sigl. & Carm.	Sigler & Carmichael (1976)
2.3.1.	Nannizzia borelli Mor., Pad. & Ajel.	
	= Microsporum amazonicum Mor., Pad. & Ajel.	Moraes, Padhye & Ajello (1975)

2.3.1.	N. cajetana Ajello = Microsporum cookei Ajello	Moraes, Padhye & Ajello (1975)
2.3.1.	N. fulva Stockdale = Microsporum fulvum Uriburu	Stockdale (1965)
2.3.1.	N. grubyia Georg, Ajello, Fried. & Brink. = Microsporum vanbreuseghemi Georg, Ajello, Fried. & Brink.	Stockdale (1965)
2.3.1.	N. gypsea Stockdale = Microsporum gypseum (Bodin) Guiant & Grig.	Stockdale (1965)
2.3.1.	N. incurvata Stockdale = Microsporum gypseum (Bodin) Guiant & Grig.	Stockdale (1961)
2.3.1.	N. obtusa Dawson & Gentles = Microsporum nanum Fuentes	Stockdale (1965)
2.3.1.	N. persicolor Stockd. = Microsporum persicolor Stockd.	Stockdale (1963)
2.3.1.	N. racemosa Rush-Munro, Smith & Borelli = Microsporum racemosum Borelli	Rush-Munro, Smith & Borelli (1970)
2.2.1.	Nanoscypha tetraspora (Seaver) Denison = unnamed hyphomycete with 'blastospores' on vegetative hyphae	Pfister (1973)
2.3.1.	Nectria apocyni Peck = Dendrodochium sp..	Samuels (1976)
2.3.1.	N. arenuloides Samuels = Acremonium sp.	Samuels (1976)
2.3.1.	N. aurantiaca (Tul.) Jacz. = [?] Sphaeropsis sp. = Stilbella cinnabarina (Mont.) Wollenw.	Booth (1959), Samuels & Rossman (Chap. 11)
2.3.1.	N. aurantiicola B. & Br. = Fusarium larvum Fuckel	Booth (1971)
2.3.1.	N. aureo-fulva Cooke & Ellis = Dendrodochium sp.	Samuels (1976)
	N. bactrioides Berk. & Br. = Myrothecium sp.	
2.3.1.	N. brassicae Ell. & Sacc. = Fusarium sp.	Booth (1959)
2.3.1.	N. byssicola B. & Br. = Dendrodochium sp.	Samuels (1976)
2.3.1.	N. candicans (Plowr.) Samuels = Acremonium sp.	Samuels (1973)
2.3.1.	N. cinnabarina (Tode ex Fr.) Fr. = Tubercularia vulgaris Tode	Dingley (1957), Booth (1959)
2.3.1.	N. coccinea (Pers. ex Fr.) Fr. = Cylindrocarpon sp.	Booth (1959)
2.3.1.	N. consors Ell. & Ev. = Volutella ciliata (Alb. & Schw.) Fr.	Samuels (1977)
2.3.1.	N. coprosma Dingley = Cylindrocarpon sp.	Dingley (1957)
2.3.1.	N. cosmariospora Ces. & de Not. = Verticillium olivaceum Gams	Gams (1971)
2.3.1.	N. cyathea Dingley = Acremonium sp.	Dingley (1956), Samuels (1976)
2.3.1.	N. dentifera Samuels = Acremonium sp.	Samuels (1976)
2.3.1.	N. desmazierii Becc. & de Not. = Fusarium buxicola Sacc.	Booth (1959)
2.3.1.	N. ellisii Booth = Acremonium sp.	Booth (1959)
2.3.1.	N. episphaeria (Tode ex Fr.) Fr. = Fusarium aquaeductuum Lagerheim var. medium Wollenw.	Booth (1959)

2.3.1.	N. flammea (Tul.) Dingley	
	= Fusarium coccophilum (Desm.) Wollenw. & Reink.	
2.3.1.	N. flavo-lanata B. & Br.	
	= Kutilakesopsis macalpineae Agnih. & Barua	Nag Raj & Govindu (1969)
	= Stromatographium sp.	
	N. flavo-viridis (Fckl.) Wollenw.	
	= Fusarium melanochlorum Casp.	Booth (1959,1971)
2.3.1.	N. fragilis Dingley	
	= Cylindrocarpon sp.	Dingley (1957)
2.3.1.	N. freycinetii Samuels	
	= Acremonium sp.	Samuels (1976)
2.3.1.	N. fuckeliana Booth	
	= Acremonium sp.	
	= Cylindrocarpon cylindroides Wollenw. var. tenue Wollenw.	Gams (1971)
	N. fuckeliana Booth var. macrospora (Wollenw.) Booth	
	= Cylindrocarpon cylindroides Wollenw.	Booth (1959,1971)
2.3.1.	N. galligena Bres. ex Stras.	
	= Cylindrocarpon mali (Allsch.) Wollenw.	Dingley (1957)
2.3.1.	N. haematococca B. & Br.	
	= Fusarium solani (Mar.) Sacc.	Samuels (1976)
2.3.1.	N. hederae Booth	
	= Acremonium sp.	
	= Cylindrocarpon sp.	Booth (1959)
	N. hirsuta Samuels	
	= Stilbella tomentosa (Schrad. ex Fr.) Bres. var olivispora (A.L. Smith) Rogerson	Samuels (1973)
2.3.1.	N. illudens Berk. in Hook	
	= Fusarium illudens Booth	Dingley (1957), Booth (1971)
	N. inventa Pethyb.	
	= Verticillium cinnabarinum (Cda.) Rein. & Berth.	Booth (1959), Shaw (1973)
2.3.1.	N. keithii B. & Br.	
	= Gliocladium vel aff.	Booth (1959,1971)
2.3.1.	N. kowhai Dingley	
	= Gliocladium vel aff.	Dingley (1957)
2.3.1.	N. laeticolor B. & C.	
	= Fusarium coccophilum (Desm.) Wollenw. & Reink.	Dingley (1957)
	N. leptosphaeriae Niessl	
	= Fusarium sphaeriae Fuckel	Booth (1959)
	N. lugdunensis Webster	
	= Heliscus lugdunensis Sacc. & Ther.	Webster (1959)
2.3.1.	N. macrostoma B. & C.	
	= Graphium vel aff.	Dingley (1957)
2.3.1.	N. magnusiana Rehm ex Sacc.	
	= Fusarium epistromum (Höhn.) Booth	
2.3.1.	N. mammoidea Phil. & Plowr. var. rubi (Osterw.) Weese	
	= Cylindrocarpon janthothele Wollenw.	Booth (1959)
2.3.1.	N. mammoidea Phill. & Plowr. var. rugulosa Weese	
	= Cylindrocarpon sp.	Booth (1959)
2.3.1.	N. manuka Dingley	
	= Acremonium sp.	Samuels (1976)
2.3.1.	N. myxomyceticola Samuels	
	= Verticillium rexianum (Sacc.) Sacc.	Samuels (1973)
2.3.1.	N. ochroleuca (Schw.) Berk.	
	= Acremonium sp.	
	= Gliocladium roseum Bain.	Dingley (1957), Samuels (1976)

2.3.1.	N. oropensoides Rehm in Bref. & Tavel = Acremonium sp.	Samuels (1976)
2.3.1.	N. otagensis Curr. ex Lind. = Aschersonia sp.	Dingley (1957)
2.3.1.	N. pallidula Cke. = Gliocladium sp.	Booth (1959)
	N. penicillioides Ranzoni = Flagellospora penicillioides Ingold	Ranzoni (1956)
	N. peristomialis (Berk. & Br.) Samuels = Acremonium sp.	Samuels (1976)
2.3.1.	N. pertusa Pat. in Pat. & Lager = Acremonium sp.	Samuels (1976)
2.3.1.	N. pertusoides Samuels = Acremonium sp.	Samuels (1976)
2.3.1.	N. peziza (Tode ex Fr.) Fr. = Acremonium sp.	Samuels (1976)
2.3.1.	N. phormiicola Sam. = Acremonium sp.	Samuels (1976)
2.3.1.	N. pinea Dingley = Cylindrocarpon sp.	Dingley (1957)
2.3.1.	N. punicea (Kze. & Schm.) Fr. = Cylindrocarpon album (Sacc.) Wollenw.	Dingley (1957)
2.3.1.	N. purtoni (Grev.) Berk. = Fusarium aquaeductuum Lagerheim	Samuels (1976)
2.3.1.	N. ralfsii B. & Br. = [?] Sphaeropsis henriquesii Thüm.	Rilestone (1941), Dingley (1957)
	N. ramulariae (Wollenw.) E. Müller = Cylindrocarpon obtusisporum (Cooke & Harkn.) Wollenw.	
2.3.1.	N. sinopica Fr. = Zythiostroma mougeotii (Fr.) Höhn.	Booth (1959)
2.3.1.	N. solani Reinke & Berthold = Gliocladium sp.	Booth (1959)
2.3.1.	N. rishbethii Booth = Acremonium sp.	Gams (1971)
2.3.1.	N. sporangiicola Samuels = Gliocladium sp.	Samuels (1973)
2.3.1.	N. stenospora B. & Br. = Gliocladium vel aff.	Dingley (1957)
2.3.1.	N. subfalcata Hennings = Acremonium sp.	Samuels (1976)
2.3.1.	N. suffulta Berk. & Curt. = Acremonium sp.	Samuels (1976)
2.3.1.	N. sylvana Mout. = Acremonium vel aff.	Samuels (1976)
2.3.1.	N. tasmanica Berk. = Cylindrocarpon janthothele var. majus Wollenw.	Dingley (1957)
2.3.1.	N. tawa Dingley = Cylindrocarpon sp.	Dingley (1957)
2.3.1.	N. westlandica Dingley = Cylindrocarpon sp.	Dingley (1957)
2.3.1.	N. ventricosa Booth = Fusarium ventricosum Appel & Wollenw.	Booth (1971)
2.3.1.	N. veuillotiana Roum. & Sacc. = Cylindrocarpon candidulum (Sacc.) Wollenw.	Booth (1971)
2.3.1.	N. violacea (Fr.) Fr. = Acremonium fungicola (Sacc.) Samuels	Samuels (1953)
2.3.1.	N. viridescens Booth = Acremonium butyri (van Beyma) Gams	Booth (1959), Gams (1971)
2.3.1.	N. vulpina (Cke.) Ell. = Acremonium sp.	Samuels (1976)

2.3.1.	N. zealandica Cke.	
	= Fusarium sp.	Dingley (1957)
2.2.1.	N. zonata Seaver	
	= Verticillium sp.	Seaver (1910), Samuels (1976)
	Nectria spp.	
	= Calostilbella sp.	
	= Stilbella sp.	
	= Stromatographium sp.	Samuels (1976), Samuels & Rossman (Chap. 11)
	Nectriella robergei Müller & Arx	
	= Illosporium sp.	Müller & Arx (1973)
	Nectriopsis candicans (Plowr.) Maire	
	= Acremonium sp.	Gams (1971)
2.3.1.	N. solani (Reinke & Reth.) Booth	
	= Cylindrocarpon sp.	Booth (1959)
	= chlamydospores	
	N. violacea (Schm. ex Fr.) Maire	
	= Acremonium sp.	Gams (1971)
	Nectriopsis sp.	
	= Fusarium sp.	Arx (1970)
	Nematospora coryli Peg.	
	= Candida sp. cf. Torulopsis sp.	Tubaki (1958)
	Nematostoma artemisiae H. & P. Sydow	
	= [?] Chaetosticta sp.	Barr (1968)
	N. occidentalis (Ell. & Ev.) Barr.	
	= Chaetosticta perforata (Ell. & Ev.) Petrak & H. Sydow	Barr (1968)
2.2.2.	Nematothecium vinosum Syd.	
	= Atractilina sp.	Hansford (1941), Pirozynski (1976)
2.3.1.	Neocosmospora africana Arx	
	= Acremonium vel aff.	Arx (1955)
2.3.1.	N. vasinfecta E.F. Smith	
	= Acremonium vel aff.	
	= Fusarium sp.	Bertoni et al. (1973)
2.3.1.	Neosartorya aurata (Warcup) Mall. & Cain	
	= Aspergillus auratus Warcup apud Raper & Fennell	Raper & Fennell (1965), Malloch & Cain (1972)
2.3.1.	N. aureola (Fenn. & Rap.) Mall. & Cain	
	= Aspergillus aureolus Fenn. & Rap.	Fennell & Raper (1955), Malloch & Cain (1972)
2.3.1.	N. citrispora Mall. & Cain	
	= Aspergillus citrisporus Höhn.	Malloch & Cain (1972)
2.3.1.	N. fischeri (Wehmer) Mall. & Cain	
	= Aspergillus fischeri Wehmer	Fennell & Raper (1955), Malloch & Cain (1972)
2.3.1.	N. fischeri (Wehmer) Mall. & Cain var. glabra (Fenn. & Rap.) Mall. & Cain	
	= Aspergillus fischeri Wehm. var. glabra Fenn. & Rap.	Malloch & Cain (1972)
2.3.1.	N. fischeri (Wehm.) Mall. & Cain var. spinosa (Rap. & Fenn.) Mall. & Cain	
	= Aspergillus fischeri Wehm. var. spinosus Rap. & Fenn.	Malloch & Cain (1972)
2.3.1.	N. fischeri (Wehmer) Mall. & Cain var. verrucosa (Udag. & Kawas.) Mall. & Cain	
	= Aspergillus sp.	Malloch & Cain (1972)
2.3.1.	N. ornata (Rap., Fenn. & Tres.) Mall. & Cain	
	= Aspergillus ornatus Rap. & Fenn.	Malloch & Cain (1972)
2.3.1.	N. quadricincta (Yuill) Mall. & Cain	
	= Aspergillus quadricinctus Yuill	Malloch & Cain (1972)
2.3.1.	N. stramenia (Nov. & Rap.) Mall. & Cain	
	= Aspergillus stramenius Nov. & Rap. in Rap. & Fenn.	Malloch & Cain (1972)

2.3.1.	Neoxenophila foetida Apinis & Clark	
	= Chrysosporium foetidum Apinis & Clark	Apinis & Clark (1974)
2.3.1.	Neurospora crassa Shear & Dodge	
	= Monilia sp.	Faull (1930)
2.3.1.	N. sitophila (Mont.) Sacc.	
	= Monilia sitophila (Mont.) Sacc.	Hashmi, Morgan-Jones & Kendrick (1972)
2.3.1.	N. tetrasperma Shear & Dodge	
	= Monilia sp.	Müller & Arx (1973)
2.3.1.	Niesslia coloradensis (Cash & Dav.) Gams	
	= Monocillium nordinii (Bour.) Gams	Gams (1971)
2.3.1.	N. exigua (Sacc.) Kirscht.	
	= Monocillium sp.	Gams (1971)
2.3.1.	N. exilis (Alb. & Schw. per Fr.) Wint.	
	= Monocillium sp.	Gams (1971)
2.3.1.	N. exosporioides (Desm.) Wint.	
	= Monocillium granulatum (Fckl.) Gams	Gams (1971)
	Nigrosabulum globosum Mall. & Cain	
	= Acremonium sp.	Malloch & Cain (1970)
2.3.1.	Nummularia broomeiana (B. & C.) J.H. Miller	
	= Xylocladium vel aff.	Rogers (1975)
2.3.1.	Nummulariola sp.	
	= Nodulisporium sp.	Martin (1969), Arx (1974)
2.2.2.	Ocellaria ocellata (Pers.) Schroet.	
	= Cryptosporiopsis scutellata (Otth.) Petr.	
	= [?] Myxosporium scutellatum Höhn.	Grove (1937), Arx (1974)
2.2.2	Ombrophila alniella Boud.	
	= Acleistia alniella Bayliss-Elliott	Bayliss-Elliott (1916)
2.3.1.	Onygena corvina Alb. & Schw.	
	= Sporendonema vel aff.	
	= synnematous hyphomycete w. arthrospores	Tubaki (1960)
2.3.1.	O. equina Pers. ex Fr.	
	= arthrospores on simple conidiophores or synnemata	Malloch & Cain (1971)
	Ophiocordyceps sp.	
	= Hirsutella sp.	Morris (1963)
	Ophionectria coccorum Petch	
	= Peziotrichum sp.	Ainsworth et al. (1971)
	O. cylindrothecia Seaver	
	= Helicomyces roseus Link	Seaver (1909)
2.3.1.	O. trichospora (B. & C.) Sacc.	
	= Antipodium spectabile Piroz.	Pirozynski (1974)
	Ophionectria sp.	
	= Helicosporium sp.	Hughes (1958)
2.3.1.	Ophiostoma epigloeum (Guer.) de Hoog	
	= Sporothrix sp.	de Hoog (1974)
2.3.1.	O. longirostellatum (Bakshi) Arx & Müller	
	= Sporothrix sp.	de Hoog (1974)
2.3.1.	O. microsporum (Dav.) Arx	
	= Sporothrix sp.	de Hoog (1974)
2.3.1.	O. multiannulatum (Hedg. & Dav.) Arx	
	= Sporothrix sp.	de Hoog (1974)
2.3.1.	O. narcissi Limber	
	= Sporothrix sp.	de Hoog (1974)
2.3.1.	O. nigrocarpum (Dav.) Arx	
	= Sporothrix sp.	de Hoog (1974)
2.3.1.	O. perfectum (Dav.) de Hoog	
	= Sporothrix sp.	de Hoog (1974)
2.3.1.	O. piceae (Münch) H. & P. Syd.	
	= Graphium sp.	
	= Sporothrix sp.	de Hoog (1974)
2.3.1.	O. piliferum (Fr.) H. & P. Syd.	
	= [?] Acrodontium simplex (Mang.) de Hoog	de Hoog (1974)

2.3.1.	O. stenoceras (Robak) Melin & Nannf. = Sporothrix schenckii Hekt. & Perk.	de Hoog (1974)
2.3.1.	O. tetropii Math. = Sporothrix sp.	de Hoog (1974)
2.3.1.	O. ulmi (Buism.) Nannf. = Graphium sp. = Sporothrix sp.	de Hoog (1974)
2.3.1.	Orbilia coccinea (Somm.) Karst. = Dicranidion sp.	Brefeld (1891), Berthet (1964)
2.3.1.	O. xanthostigma (Fr.) Fr. = Dicranidion sp.	Berthet (1964)
	Orbiliella sp. = [?] Trichothecium sp.	Korf (1973)
	Ovulinia azaleae Weiss. = Ovulitis azaleae Buchw.	Buchwald (1949)
2.3.1.	Parkerella populi Funk = Cladorrhinum vel aff. = Cyphellophora vel aff.	Funk (1976)
1.1.	Peckiella banningiae (Peck) Sacc. = Acremonium sp. or Sepedonium sp.	Arnold (1971)
1.1.	P. camphorata (Peck) Seaver = Acremonium sp. or Sepedonium sp.	Arnold (1971)
1.1.	P. completa G. Arnold = Acremonium sp. or Sepedonium sp.	Arnold (1971)
1.1.	P. hymenii Peck = Acremonium sp. or Sepedonium sp.	Arnold (1971)
1.1.	P. lateritia (Fr.) Maire = Acremonium sp. or Sepedonium sp.	Arnold (1971)
1.1.	P. luteo-virens (Fr.) Maire = Acremonium sp. or Sepedonium sp.	Arnold (1971)
1.1.	P. torminosa (Dur. & Mont.) Maire = Acremonium sp. or Sepedonium sp.	Arnold (1971)
1.1.	P. transformans (Peck) Sacc. = Acremonium sp. or Sepedonium sp.	Arnold (1971)
2.3.1.	Peloronectriella sasae Doi = [?] Acremonium sp.	Gams (1971)
2.3.1.	Penicilliopsis clavariaeformis Solms-Laubach = Penicillium vel aff.	Fennell (1973)
2.3.1.	Penzigia frustulosa (Berk. & curt.) J.H. Miller = unnamed sporodochial hyphomycete	Jong & Rogers (1970)
	Peroneutypella echidna (Cke.) Deighton = Phaeoisaria sp.	Deighton (1974)
2.2.2.	Pestalosphaeria concentrica Barr = Pestalotiopsis guepini (Desm.) Stey. var. macrotricha Sutton	Barr (1975)
2.3.1.	Pestalopezia brunneo-pruinosa (Zeller) Seaver = Pestalotia gibbosa Harkness	Bonar (1942)
2.3.1.	P. tsugae Funk = [?] Seiridium abietinum (Ell. & Ev.) Sutton	Funk (1978)
2.3.1.	Petriella guttulata Barron & Cain apud Barron, Gilm. & Cain = Graphium sp.	Barron, Gilman & Cain (1961)
2.3.1.	P. lindforsii Curzi = Graphium sp.	Curzi (1930), Barron, Gilman & Cain (1961)
2.3.1.	P. setifera (Schm.) Curzi = Graphium sp.	Barron, Gilman & Cain (1961)
2.3.1.	P. musispora Mall. = Scopulariopsis sp.	Malloch (1970)
2.3.1.	Petriellidium angustum Mall. & Cain = Graphium vel aff.	Malloch & Cain (1972)
2.3.1.	P. boydii (Shear) Mall. = Scedosporium apiospermum (Sacc.) Sacc.	Malloch (1970), Arx (1973)

2.3.1.	P. fusoideum Arx	
	= Scedosporium sp.	Arx (1973)
	Petromyces alliaceus Mall. & Cain.	
	= Aspergillus alliaceus Thom & Church	Malloch & Cain (1972)
	Pezicula acericola (Peck) Sacc.	
	= Cryptosporiopsis sp.	Seaver (1951)
	P. alba Guthrie	
	= Phlyctaena vagabunda Desm.	Arx (1970)
2.2.2.	P. alni Rehm	
	= unnamed coelomycete [?] phialidic	Seaver (1951)
2.2.2.	P. alnicola Groves	
	= unnamed coelomycete [?] phialidic	Seaver (1951)
2.	P. aurantiaca Rehm	
	= Cryptosporiopsis sp.	Groves (1940)
2.2.2.	P. carpinea (Pers.) Tul.	
	= Cryptosporiopsis fasciculata Petr.	
	= [?] Myxosporium sp.	
	= [?] Sphaeronaema sp.	Seaver (1951)
2.3.1.	P. carnea (C. & E.) Rehm	
	= Cryptosporiopsis sp.	Groves (1941)
	P. cinnamomea (DC.) Sacc.	
	= Cryptosporiopsis grisea (Pers.) Petr.	C.B.S. catalogue, Groves (1941)
	P. corni Petrak	
	= Cryptosporiopsis cornina Petr. & Syd.	Seaver (1951)
2.2.2.	P. cornicola Seaver	
	= "Myxosporium sp."	Seaver (1951)
	P. corticola (Jorg.) Nannf.	
	= Cryptosporiopsis corticola Jorg.	
	= Myxosporium corticola Edj.	Nannfeldt (1932)
2.2.2.	P. corylina Groves	
	= Catinula turgida (Fr.) Desm.	Seaver (1951), Shaw (1973)
	P. frangulae (Pers.) Fuckel	
	= Cryptosporiopsis versiformis (Alb. & Schw.) Wollenw.	Wollenweber (1939)
2.2.2.	P. hamamelidis Groves & Seaver	
	= Cryptosporiopsis sp.	Seaver (1951)
	P. livida (B. & Br.) Rehm	
	= Myxosporium abietinum Rostr.	Seaver (1951)
2.3.1.	P. morthieri (Fuckel) Groves	
	= [?] Sphaerographium niveum Dearn. & House	Groves (1947), Seaver (1951)
	P. ocellata (Pers.) Seaver	
	= [?] Cryptosporiopsis sp.	Seaver (1951)
	P. populi (Thompson) Seaver	
	= "Myxosporium sp."	Seaver (1951)
2.2.2.	P. purpurascens (Ell. & Ev.) Seaver	
	= Ascoconidium castaneae Seaver	Seaver (1951)
	P. pruinosa (Peck) Farlow	
	= Sphaeronaema pruinosa Peck	Seaver (1933,1951)
	P. rubi (Libert) Rabenh.	
	= Myxosporium phaeosorum (Sacc.) All.	Grove (1937), Seaver (1951), Arx (1970)
2.2.2.	P. spiculata Seaver	
	= Sphaeronaema sp.	Seaver (1933,1951)
2.3.1.	P. subcarnea Groves	
	= Cryptosporiopsis sp.	Groves (1941)
2.3.1.	P. ampliata Pers. ex Pers.	
	= Oedocephalum sp.	Brefeld (1891), Paden (1972)
2.3.1.	Peziza anthracophila Dennis	
	= Oedocephalum sp.	Webster et al. (1964)
2.3.1.	P. anthracina Cke.	
	= Chromelosporium sp.	Paden (1972)
2.3.1.	P. brunneoatra Desm.	
	= unnamed holoblastic hyphomycete	Paden (1967)

2.3.1.	P. cerea Sow.	
	= Oedocephalum sp.	Brefeld (1891), Paden (1972)
2.3.1.	P. endocarpoides Berk. in Hook.	
	= Chromelosporium sp.	Hennebert (1973)
2.3.1.	P. leiocarpa Curr.	
	= Chromelosporium sp.	Paden (1972)
2.3.1.	P. oenotherae (Cke. & Ell.) Sacc.	
	= Hainesia lythri (Desm.) Höhn.	C.B.S. catalogue
2.3.1.	P. ostracoderma Korf	
	= Chromelosporium ollare (Pers.) Henneb.	Hennebert (1973), Hennebert & Korf (1975)
2.3.1.	P. petersii Berk. & Curt.	
	= Oedocephalum sp. and 'aleuriospores'	Paden (1972)
2.3.1.	P. praetervisa Bres.	
	= Oedocephalum sp.	Webster et al. (1964)
2.3.1.	P. pustulata Pers.	
	= Oedocephalum sp.	Dodge (1937)
	P. quelepidotia Korf & O'Donnell	
	= Botrytis vel aff.	O'Donnell et al. (1976)
2.3.1.	P. repanda Pers.	
	= Oedocephalum sp.	Paden (1972)
2.3.1.	P. saniosa Fr.	
	= 'aleuriospores'	Paden (1972)
2.3.1.	P. trachycarpa Curr.	
	= Chromelosporium trachycarpum Henneb.	Hennebert (1973)
	P. vesiculosa Bull.	
	= Oedocephalum sp.	Paden (1972)
2.2.2.	Phacidium cicatricolum Fckl.	
	= Ceuthospora cicatricola Höhn.	Höhnel (1925), Nannfeldt (1932)
2.2.2.	P. cytisi Fckl.	
	= Ceuthospora cystissi Höhn.	Höhnel (1925), Nannfeldt (1932)
2.2.2.	P. falconeri Henn.	
	= Ceuthospora rhododendri Gr.	
2.2.2.	P. gracile Niessl (≡ Phacidina gracilis (Niessl) Höhn.)	
	= Ceuthospora lycopodii Lind.	Höhnel (1925)
2.2.2.	P. lacerum Fr.	
	= Ceuthospora pinastri (Fr.) Höhn.	Höhnel (1925)
2.2.2.	P. multivalve (DC.) Schm.	
	= Ceuthospora phacidioides Grev.	Höhnel (1925)
2.2.2.	P. pyrolae Karst.	
	= Ceuthospora pyrolae (Karst.) Höhn.	Höhnel (1925)
2.2.2.	P. salicinum Fckl.	
	= Ceuthospora salicina Höhn.	Höhnel (1925)
2.2.2.	P. taxi Fr.	
	= Ceuthospora taxi (Died.) Höhn.	Höhnel (1925)
2.2.2.	P. vaccinii Fr.	
	= Ceuthospora latitans (Fr.) Höhn.	Höhnel (1925)
2.2.2.	P. vincae Fckl.	
	= Ceuthospora foliicola (Lib.) Jaap.	Höhnel (1925)
	Phanerococcus sp.	
	= Phanerococculus sp.	Ainsworth et al. (1971)
2.2.2.	Pharcidia laminaricola Kohlmeyer	
	= unnamed coelomycete	Kohlmeyer (1972)
2.2.2.	P. rhachiana Kohlm.	
	= unnamed coelomycete	Kohlmeyer (1973)
2.2.2.	Phialea temulenta Prill. & Delacr.	
	= Endoconidium temulentum Prill & Delacr.	Nag Raj & Kendrick (1975)
2.3.1.	Phillipsia guatemalensis Paden	
	= Blastobotrys vel aff.	Paden (1977)
2.3.1.	P. rugospora Paden	
	= unnamed sympodial hyphomycete	Paden (1977)
2.2.2.	Phomatospora berkeleyi Sacc.	
	= Phoma berkeleyi Sacc.	Grove (1935)

2.3.1.	P. dinemasporium Webster	
	= Dinemasporium gramineum (Lib.) Lév.	Webster (1955)
1.1.	Phyllachora agrostidis Fckl.	
	= Placosphaeria graminis Sacc. & Roum.	Grove (1935)
1.1.	P. angelicae Fckl.	
	= Phyllosticta angelicae Sacc.	Grove (1935)
2.2.1.	P. graminis Fckl.	
	= Leptostromella graminis Gr.	Grove (1937)
1.1.	P. heraclei Fckl.	
	= Phloeospora heraclei Petrak	Grove (1935)
2.2.2.	P. silvatica Sacc.	
	= Placosphaerella silvatica Sacc.	Grove (1935)
1.1.	P. stellariae Lib.	
	= Leptostroma stellariae Kir.	Grove (1937)
2.2.2.	Phyllactinia dalbergiae Piroz.	
	= Ovulariopsis sp.	Pirozynski (1965)
2.2.2.	P. guttata (Wallr. ex Fr.) Lév.	
	= Oidium sp.	Kapoor (1967)
2.3.1.	Physalospora fusca Stev.	
	= [?] Diplodia sp.	Stevens (1918)
2.2.1.	P. gregaria Sacc.	
	= [?] Diplodina salicicola Sacc. & Trav.	
	= Dothiorella gregaria Sacc.	
	= Phyllostictina hystrella (Sacc.) Petr.	
	= Stagonospora salicicola Sacc. & Trav.	Grove (1935), Shaw (1973)
2.3.1.	P. malorum Peck	
	= [?] Sphaeropsis malorum Peck	Shear, Stevens & Wilcox (1925)
1.1.	P. minutula Sacc. & Speg.	
	= Phoma cyclospora Sacc.	Grove (1937)
1.1.	P. miyabeana Fukushi	
	= Myxosporium sp.	Grove (1937)
	P. mutila N.E. Stevens	
	= Diplodia mutila (Fr.) Mont.	Stevens (1936), Shaw (1973)
1.1.	P. phormii Schröt.	
	= Pirostoma viridisporum Gr.	Grove (1937)
2.3.1.	P. rhodina (Berk. & Curt) Cke.	
	= Botryodiplodia theobromae Pat.	Stevens (1926)
1.1.	P. rosicola Sacc.	
	= Phoma aculeorum Sacc.	Grove (1937)
	P. tucumanensis Speg.	
	= Colletotrichum falcatum Went.	American Type Culture Collection Catalogue
2.2.2.	[?] P. zeae Stout	
	= Macrophoma zeae Tehon & Daniels	Stout (1930)
	Physalospora sp.	
	= Arthrinium sp.	Arx (1974)
2.3.1.	Pichia sp.	
	= Candida sp.	Tubaki (1958)
2.3.1.	P. crossotarsi Batra	
	= unnamed blastic hyphomycete	Batra (1971)
2.3.1.	P. microspora Batra	
	= [?] Candida sp.	Batra (1971)
	Pithya cupressina (Fr.) Fckl.	
	= Botrytis vel aff.	Paden (1972)
	Plectania nannfeldtii Korf	
	= Conoplea sp.	Paden (1972)
2.3.1.	Plectosphaera spartii Müller	
	= pycnidioid coelomycete (not Myxormia sp. fide Nag Raj & DiCosmo)	Müller (1957)
	Plectosphaerella sp.	
	= Fusarium sp.	Gams & Gerlagh (1968)
2.2.2.	Pleochaeta polychaeta (Berk. & Curt. in Berk.) Kimbrough & Korf	
	= Ovulariopsis bonariensis (Speg.) Speg.	Pirozynski (1965)

2.2.2.	P. shirainana (Henn.) Kimbr. & Korf	
	= Ovulariopsis sp.	Pirozynski (1965)
	Pleocryptospora bambusae (Speg.) Reid & Cain	
	= ascospores bud in ascus	Reid & Cain (1969)
	Pleonectria berolinensis Sacc.	
	= Dendrodochium berolinense Wr.	Shaw (1973)
	Plicaria fulva Schneider	
	= Acladium sp.	Schneider (1954), Wolf (1958)
2.2.4.	Podosphaera clandestina (Wallr. ex Fr.) Lév.	
	= Oidium sp.	Khairi & Preece (1969)
2.2.4.	P. leucotricha (Ell. & Ev.) Salm.	
	= Oidium farinosum Cke.	
	= Oidium mespili Cke.	Kapoor (1967)
2.2.4.	P. tridactyla (Wallr.) de Bary	
	= Oidium passerinii Bert.	Mukerji (1968)
2.2.4.	Podospora aloides (Fckl.) Mirza & Cain	
	= Phialophora vel aff.	Mirza & Cain (1969)
2.2.4.	P. anserina (Ces. in Rabenh.) Niessl	
	= Phialophora vel aff.	Mirza & Cain (1969)
2.2.4.	P. australis (Speg.) Niessl	
	= Phialophora vel aff.	Mirza & Cain (1969)
2.2.4.	P. austro-americana (Speg.) Mirza & Cain	
	= Phialophora vel aff.	Mirza & Cain (1969)
2.2.4.	P. communis (Speg.) Niessl	
	= Phialophora vel aff.	Mirza & Cain (1969)
2.2.4.	P. curvula (de Bary) Niessl	
	= Phialophora vel aff.	Furuya & Udagawa (1972)
2.2.4.	P. fimbriata (Bayer) Cain	
	= Phialophora vel aff.	Mirza & Cain (1969)
2.2.4.	P. hirsuta Dang.	
	= Phialophora vel aff.	Mirza & Cain (1969)
2.2.4.	P. perplexens (Cain) Cain	
	= Phialophora vel aff.	Mirza & Cain (1969)
2.2.4.	P. spinulosa Khan & Cain	
	= Phialophora vel aff.	Mirza & Cain (1969)
2.2.4.	P. tetraspora (Winter) Cain	
	= Phialophora vel aff.	Mirza & Cain (1969)
2.2.4.	P. tarvisina (Sacc.) Cain	
	= Phialophora vel aff.	Mirza & Cain (1969)
	Podostroma alutaceum (Pers.) Atk. (sub "Podocrea alutacea")	
	= Trichoderma vel aff.	
	= Verticillium sp.	Tubaki (1958), Doi (1967)
2.3.1.	P. cordyceps (Penz. & Sacc.) Doi	
	= Trichoderma sp.	Doi (1967)
2.3.1.	P. cornu-damae (Pat.) Boed.	
	= Trichoderma vel aff.	Doi (1967)
2.3.1.	P. solmii (Fisch.) Imai	
	= Trichoderma vel aff.	Doi (1967)
2.2.1.	Polystigma rubra (Pers.) DC.	
	= Polystigmina rubra Sacc.	Alexopoulos (1940)
2.3.1.	Poronia oedipus (Mont.) Mont.	
	= Xylocladium sp.	Jong & Rogers (1969)
2.3.1.	P. pileiformis (Berk.) Fr.	
	= Nodulisporium vel aff.	Paden (1977)
2.3.1.	P. punctata (L. ex Fr.) Fr.	
	= Xylocladium sp.	Stiers, Rogers & Russell (1973)
2.3.1.	Potebniamyces balsamicola Smer.	
	= Phacidiopycnis balsamicola Funk	Funk (1969,1970)
	= P. boycei (Hahn) Funk	Hahn (1957), Smerlis (1962)

2.3.1.	P. coniferarum (Hahn) Smerlis = Phacidiopycnis pseudotsugae (Wil.) Hahn	Hahn (1957), Smerlis (1962), Funk (1969,1970)
2.3.1.	P. discolor (Mouton & Sacc.) Smerlis = Phacidiopycnis furfuracea (Rostrup) Jorst. = Fuckelia sp.	Hahn (1957), Smerlis (1962), Funk (1969,1970)
	Potebniamyces sp. = Aureobasidium vel aff. = Hormonema vel aff.	Hermanides-Nijhof (1977)
2.2.2.	Pragmopora pithya (Fr.) Groves = Pragmopycnis pithya Sutt. & Funk	Sutton & Funk (1975)
2.2.1.	Propolis rhodoleuca Fr. = Pseudopatellina conigena Höhn.	Grove (1937)
2.2.2.	Prosthecium berkeleyi (Tul.) Wehmeyer = Dothiorella convergens (Tode) Höhn. = Hendersonia berkeleyi Sacc. = Stilbospora macrosperma Berk. & Br.	Wehmeyer (1941)
2.2.2.	P. ellipsosporum Fres. = Stilbospora sp.	Wehmeyer (1941)
2.2.2.	P. innesii (Curr.) Wehmeyer = Phomopsis platanoidis (Cke.) Died	Wehmeyer (1941)
2.2.2.	P. stylosporum (Ell. & Ev.) Wehmeyer = [?] Phomopsis vel aff.	Wehmeyer (1941)
2.3.1.	P. ulmi Wehmeyer = [?] Phomopsis vel aff.	Wehmeyer (1941)
2.3.1.	Pseudeurotium luteolum Mats. = Geotrichum sp.	Matsushima (1975)
	P. ovalis Stolk = Sporothrix sp.	Stolk (1955)
2.3.1.	P. punctatum Panasenko = [?] Sporothrix sp.	
2.3.1.	P. zonatum van Beyma = Sporothrix sp.	Fennell (1973), Matsushima (1975)
2.3.1.	Pseudoguignardia scirpi Gutner = Arthrinium curvatum Knze. ex Fr.	Cooke (1954)
2.3.1.	Pseudogymnoascus roseus Raillo = Geomyces vinaceus Dal Vesco	Samson (1972), Sigler & Carmichael (1976)
	Pseudomassaria carolinensis Barr & Hodges = Beltraniella portoricensis (Stev.) Piroz. & Patil	Hodges & Barr (1971)
	Pseudonectria tilachlidii Gams = Tilachlidium brachiatum (Batsch per Fr.) Petch	
	P. pachysandricola Dodge = Volutella pachysandricola Dodge	
	P. rousselliana (Mont.) Seav. = Volutella buxi (Corda) Berk.	
	Pseudonectria sp. = Sesquicillium sp.	Arx (1971)
2.2.2.	Pseudopeziza eucalypti Hansf. = Gloeosporiella eucalypti Hansf.	Hanford (1956)
1.1.	P. jaapi Rehm = Cylindrosporium padi Karst.	Grove (1937)
	P. jonesii Nannf. = Sporonema phacidioides Desm.	Schüepp (1959)
	P. ribis Rehm. in Kleb. = Gloeosporidiella ribis (Lib.) Petr.	Grove (1937), Shaw (1973)
1.1.	P. salicis (Tul.) Potebn. = Gloeosporidiella salicis (West.) Nannf.	Shaw (1973)
1.1.	P. tiliae Kleb. = Stagonospora meliloti (Lasch.) Petr.	Grove (1937), Arx (1970)

	Pseudophacidium callunae (Karst.) = Myxofusicoccum Shear	Shaw (1973)
2.3.1.	P. gaeumannii E. Müller = Ceuthospora sp.	Müller (1963), Egger (1966)
2.3.1.	P. ledi (Alb. & Schw. ex Fr.) Karst. = Myxofusicoccum ericeti (Sacc.) Petr.	Egger (1966)
2.3.1.	P. piceae E. Müller = Myxofusicoccum sp.	Müller (1963), Egger (1966)
1.1.	Pseudovalsa haplocystis Sacc. = Fusicoccum haplocystis Sacc. = Phoma haplocystis Sacc.	Grove (1935)
2.3.1.	P. lanciformis (Fr.) Ces. & de Not. = Coryneum brachyurum Link	Sutton (1975)
2.2.2.	P. longipes (Tul.) Sacc. = Coryneum umbonatum Nees ex Steudel	Sutton (1975)
2.2.2.	P. modonia (Tul.) Höhn. = Coryneum modonium (Sacc.) Griff. & Maubl.	Sutton (1975)
2.2.2.	P. umbonata (Tul.) Sacc. = Coryneum depressum Schm. ex Steudel	Sutton (1975)
	Pseudovalsella tetraspora Kobayashi = Coryneum pedunculatum Kobay. (1970), non C. pedunculatum (Ell. & Ev.) Hughes	Kobayashi (1970)
2.3.1.	Pycnopeziza quisquiliaris (Ell. & Ev.) White & Whetzel = "Acarosporium quisquiliaris White & Whetzel", see International Code of Botanical Nomenclature, 1972, Art. 36.	White & Whetzel (1938)
2.3.1.	P. sympodialis White & Whetz., (see International Code of Botanical Nomenclature, 1972, Art. 59) = Acarosporium sympodiale Bub. & Vl.	White & Whetzel (1938)
1.1.	Pyrenopeziza salicis-capreae Jaap. = Marssonina salicicola Magn.	Grove (1937)
1.1.	P. plicata Rehm = Phoma conicola Elliot	Grove (1935)
	Pyrenopeziza sp. = Phialophora sp.	Korf (1973)
	Pyronema omphalodes (Bull.) Fuckel = Oedocephalum glomerulosum Harz.	Schmidt (1910), cf. Moore & Korf (1963)
	Pyxidiophora asterophora (Tul.) Lindau = Chalara vel aff. = Paecilomyces sp.	Tubaki (1958), Müller & Arx (1973)
2.2.1.	Quaternaria dissepta (Fr. ex Fr.) Tul. = Libertella dissepta Trav.	Grove (1937)
1.1.	Q. persoonii Tul. = Libertella faginea Desm.	Grove (1937), Müller & Arx (1973)
	Remispora sp. = Periconia sp.	Carmichael, Kendrick & Conners (1979)
2.2.2.	Rhabdocline pseudotsugae Syd. = Rhabdogloeum hypophyllum Ell. & Gill.	Parker & Reid (1969)
2.2.2.	R. weirii Parker & Reid = Rhabdogloeum pseudotsugae Syd.	Parker & Reid (1969)
2.3.1.	Rhizocalyx abietis Petr. = Rhizothyrium abietis Naumoff	Smerlis (1967)
2.2.2.	Rhytisma acerinum Fr. = Melasmia acerina Lév.	Grove (1937), Nannfeldt (1937)
1.1.	R. arbuti Phill. in Vize = Melasmia salicina Lév.	Shaw (1973)
2.2.2.	R. himalense Sydow & Butl. = Melasmia sp.	Nannfeldt (1932)

1.1.	R. punctatum Fr.	
	= Melasmia punctata Sacc. & Roum.	Nannfeldt (1932)
2.2.2.	R. salicinum Fr.	
	= Melasmia salicina Lév.	Grove (1937)
1.1.	R. xylostei Naum.	
	= Melasmia lonicerae A. Jacz.	Nannfeldt (1932)
2.3.1.	Rollandina vriesii Apinis	
	= Chrysosporium vel aff.	Apinis (1970)
	Rosellinia aquila (Fr.) de Not.	
	= Nodulisporium vel aff.	Tulasne & Tulasne (1863), Shear (1941), Subramanian (1956)
2.3.1.	R. buxi Fabre	
	= Nodulisporium vel aff.	Hughes (1951), cf. Rogers & Malmgren (1977)
	R. necatrix (Hartig) Berl. ex Prill.	
	= Nodulisporium vel aff. (sub Dematophora sp.)	Ellis (1971)
	R. thelena (Fr.) Raben.	
	= Nodulisporium vel aff. (= [?] Stachylidium sp.)	Hughes (1951), Subramanian (1956)
	Roumegueriella rufula (B. & Br.) Mall. & Cain	
	= [?] Gliocladium prolificum Bain.	
	= Phialocephala vel aff.	Malloch (1970)
2.3.1.	Rustroemia bolaris (Batsch ex Fr.) Rehm	
	= [?] Myrioconium sp. (spermatial)	
	= [?] Phialophora vel aff.	Berthet (1964)
2.3.1.	R. echinophila (Bull. ex Mérat) Höhn.	
	= [?] Myrioconium sp. (spermatial)	Berthet (1964)
2.3.1.	R. firma (Pers. ex Fr.) Karst.	
	= [?] Myrioconium sp. (spermatial)	
	= [?] Phialophora vel aff.	Berthet (1964)
2.3.1.	Saccharomyces sp.	
	= Candida sp. cf. Torulopsis sp.	Tubaki (1958)
2.3.1.	Sagenoma viride Stolk & Orr	
	= Acremonium sagenomatis Stolk & Orr	Stolk & Orr (1975)
2.2.2.	Sageria tsugae Funk	
	= Ascoconidium tsugae Funk	Funk (1975)
2.3.1.	Sarcoscypha coccinea (Fr.) Lamb. var. jurana Boud.	
	= Botrytis vel aff.	Alexopoulos & Butler (1949)
2.3.1.	[?] Sarcosoma latahensis Paden & Tylutki	
	= Conoplea sp.	Paden (1972)
2.3.2.	Sarcotrochila balsameae (Dav.) Korf	
	= Kabatiella balsameae (Dav.) Arx	Shaw (1973)
2.3.2.	Schizoparme straminea Shear	
	= Coniella sp. fide DiCosmo	Shear (1923)
	Sclerocleista ornata (Raper, Fennell & Tresner) Subram.	
	= Aspergillus sp.	Malloch & Cain (1973)
2.2.2.	Scleroderris lagerbergii Grem.	
	= Brunchorstia pinea (Karst.) Höhn.	Roll-Hansen & Roll-Hansen (1973)
	Sclerotinia corni Reade	
	= Monilia corni Reade	Shaw (1973)
	S. convoluta Drayton	
	= Botrytis convoluta Whetzel	Dennis (1956)
	S. draytoni Dennis & Wakef.	
	= Botrytis gladiolorum Timmerm.	Shaw (1973)
2.3.1.	S. fuckeliana (de Bary) Fuckel	
	= Botrytis cinerea Pers. ex Fr.	Dennis (1956)
2.3.1.	S. globosa (Buchwald) Webster	
	= Botrytis globosa Raabe	Dennis (1956)
2.3.1.	S. narcissicola Gregory	
	= Botrytis narcissicola Kleb.	Gregory (1941), Shaw (1973)

	S. padi Woron.	
	= Monilia linhartiana Sacc.	C.B.S. catalogue
	S. pelargonii (Roed.) Roed.	
	= Botrytis pelargonii Roed.	
2.3.1.	S. polyblastis Gregory	
	= Botrytis polyblastis Dowson	Gregory (1941), Dennis (1956)
	S. pseudotuberosa Rehm	
	= Rhacodiella castaneae (Bain.) Peyr.	
	(= Myrioconium sp. fide Carmichael 1973)	
	S. ricini God.	
	= Botrytis ricini God.	
2.2.2.	S. scirpicola Rehm	
	= Myrioconium scirpicola (Ferd. & Winge) Ferd. & Winge (spermatial state)	Ferdinandsen & Winge (1913)
	S. sclerotiorum (Lib.) de Bary	
	= Sclerotium sp.	Dennis (1968), von Arx (1974)
	S. spermophila Noble	
	= Botrytis anthophila Bond.	Dennis (1956)
2.3.1.	S. sphaerosperma Gregory	
	= Botrytis sphaerosperma Buchw.	Gregory (1941), Dennis (1956)
	S. squamosa (Vien.-Bourg.) Dennis	
	= Botrytis squamosa Walker	Dennis (1956)
	S. sulcata Whetz.	
	= Sclerotium sulcatum Rob. ex Desm.	
2.3.1.	S. tuberosa (Hedw. ex Fr.) Fckl.	
	= [?] Myrioconium sp. (spermatial state)	Berthet (1964)
	S. vaccinii-corymbosi Reade	
	= Monilia vaccinii-corymbosi Reade	
2.3.1.	Scoleconectria cucurbitula (Tode ex Fr.) Booth	
	= Zythiostroma pinastri (Karst.) Höhn.	Booth (1958)
1.1.	S. tetraspora Seav.	
	= [?] Verticillium sp.	Seaver (1928)
2.3.1.	Seaverina geranii (Seav. & Horne) Whetz.	
	= Verrucobotrys geranii (Seav.) Henneb.	Whetzel (1945), Hennebert (1973)
2.3.1.	Septotinia podophyllina Whetz.	
	= Septotis podophyllinum (Ell. & Ev.) Arx	Buchwald (1949)
2.3.2.	S. populiperda Wat. & Cash.	
	= Septotis populiperda (Moesz. & Smar.) Wat. & Cash	Cash (1950)
2.2.4.	Spathulospora phycophila Cav. & Johnson	
	= Phialidic perithecial hairs (?spermatial)	Kohlmeyer (1969)
	Sphaerognomonia carpinea (Fr.) Potebn.	
	= Monostichella robergei (Desm.) Höhn.	Grove (1937), Arx (1970)
2.3.1.	Sphaeronaemella fimicola Marchal	
	= Gabarnaudia fimicola Sams. & Gams	Samson & Gams (1971)
2.3.1.	S. humicola Sams. & Gams	
	= Gabarnaudia humicola Sams. & Gams	Samson & Gams (1971)
	Sphaerostilbe cinnabarina (Mont.) Tul.	
	= Atractium cinnabarinum Mont.	Seaver (1909)
	S. flammea (Berk. & Rav.) Tul.	
	= Atractium flammeum Berk. & Rav.	Seaver (1909)
2.2.2.	Sphaerotheca fuliginea (Schlect. ex Fr.) Poll.	
	= Oidium erysiphoides Fr.	Kapoor (1967)
2.2.2.	S. macularis (Wallr. ex Fr.) Lind.	
	= Oidium sp.	Mukerji (1968)
2.2.2.	S. pannosa (Wallr. ex Fr.) Lév.	
	= Oidium leucoconium Desm.	Mukerji (1968)
2.2.2.	Stamnaria americana Mass. & Morg.	
	= [?] Titaeospora equiseti (Desm.) Vass.	Seaver (1932), cf. Arx (1970)
	S. equiseti (Hoffm.) Sacc.	
	= [?] Titaeospora equiseti (Desm.) Vass.	Arx (1970)
	S. persoonii Fckl.	
	= [?] Titaeospora equiseti (Desm.) Vass.	Grove (1937), Arx (1970)
2.3.1.	Stephensia shanori (Gilkey) Gilkey	
	= holoblastic hyphomycete	Uecker (1967)

	Stictis sp.	
	= Fusidium sp.	Korf (1973)
2.3.1.	Streptotinia arisaemae Whetz.	
	= Streptobotrys arisaemae Henneb.	Whetzel (1945), Hennebert (1973)
2.3.1.	S. caulophylli Elliott	
	= Streptobotrys streptothrix (Cke. & Ellis) Henneb.	Elliott (1962), Hennebert (1973)
2.2.2.	Stromatinia cepivora (Berk.) Whetz.	
	= Sclerotium cepivorum Berk.	Whetzel (1945)
2.2.2.	S. gladioli (Drayt.) Whetz.	
	= Sclerotium gladioli Mass.	Whetzel (1945)
2.3.1.	S. narcissi Dray. & Groves	
	= Sclerotium ambiguum Duby var. narcissi Sacc.	Drayton & Groves (1952)
2.2.1.	Strossmayeria basitricha (Sacc.) Ed.	
	= [?] Bipolaris vel aff.	
	= [?] Helminthosporium vel aff.	Korf (1973)
2.3.1.	Subbaromyces splendens Hess.	
	= unnamed annellidic hyphomycete cf. Bainieria	Cole et al. (1974)
1.1.	Symphyosirinia sp.	
	= Symphyosira sp.	Ainsworth et al (1971)
2.3.1.	Talaromyces avellaneus (Thom. & Tur.) Benj.	
	= Penicillium avellaneum Thom. & Tur.	Benjamin (1956)
2.3.1.	T. bacillisporus (Swift) Benj.	
	= Penicillium bacillosporum Swift	Benjamin (1955), Stolk & Samson (1972)
2.3.1.	[?] T. byssochlamydoides Stolk & Sams.	
	= Paecilomyces byssochlamydoides Stolk & Sams.	Stolk & Samson (1972), Samson (1974)
2.3.1.	T. emersonii Stolk	
	= Penicillium emersonii Stolk	Stolk & Samson (1972)
2.3.1.	T. flavus (Klöcker) Stolk & Sams. var. flavus Stolk & Sams.	
	= Penicillium vermiculatum Dang.	Stolk & Samson (1972)
2.3.1.	T. helicus (Rap. & Fenn.) Benj.	
	= Penicillium helicum Rap. & Fenn.	Benjamin (1955), Stolk & Samson (1972)
2.3.1.	T. intermedius (Apinis) Stolk & Sams.	
	= Penicillium intermedium Stolk & Sams.	Stolk & Samson (1972)
2.3.1.	T. leycettanus Evans & Stolk	
	= Paecilomyces leycettanum (Ev. & Stolk) Stolk, Sams. & Evans	Evans & Stolk (1971), Samson (1974)
2.3.1.	T. luteus (Zukal) Benj.	
	= Penicillium luteum Zukal	Benjamin (1955), Stolk & Samson (1972)
2.3.1.	T. purpureus (Müller & Pacha-Aue) Stolk & Sams.	
	= Penicillium purpureum Stolk & Sams.	Stolk & Samson (1972)
2.3.1.	T. rotundus (Rap. & Fenn.) Benj.	
	= Penicillium rotundum Rap. & Fenn.	Benjamin (1955), Stolk & Samson (1972)
2.3.1.	T. stipitatus (Thom ex Emmons) Benj.	
	= Penicillium stipitatum Thom ex Emmons	Benjamin (1955), Stolk & Samson (1976)
2.3.1.	T. striatus (Rap. & Fenn.) Benj.	
	= Penicillium striatum Rap. & Fenn.	Benjamin (1955)
2.3.1.	T. tachyspermus (Shear) Stolk & Sams.	
	= Penicillium spiculisporum Lehman	Stolk & Samson (1972)
	T. thermophilus Stolk	
	= Penicillium dupontii Griff. & Maub.	Stolk & Samson (1972)
2.3.1.	T. ucrainicus (Panas.) Udagawa	
	= Penicillium ucrainicum Panas.	Stolk & Samson (1972)

2.3.1.	T. udagawae Stolk & Sams.	
	= Penicillium udagawae Stolk & Sams.	Stolk & Samson (1972)
2.3.1.	T. vermiculatus (Dang.) Benj.	
	= Penicillium vermiculatum Dang.	Benjamin (1955), cf. Stolk & Samson (1972)
2.3.1.	T. wortmannii (Klöcker) Benj.	
	= Penicillium wortmanni Klöcker	Benjamin (1955), Stolk & Samson (1972)
2.3.1.	Tapesia cinerella Rehm	
	= Cystodendron sp.	Aebi (1972)
2.3.1.	T. fusca (Pers. ex Fr.) Fckl.	
	= Cystodendron sp.	Aebi (1972)
2.3.1.	T. hydrophila (Karst.) Rehm	
	= Cystodendron sp.	Aebi (1972)
	T. villosa Aebi	
	= Cystodendron sp.	Aebi (1972)
	Taphrina sp.	
	= Rhodotorula sp.	Hennebert (1971)
	Tarzetta sp.	
	= Oedocephalum sp.	Cain & Hastings (1956)
	Thaxteria fusca (Fckl.) Booth	
	= Oedemium atrum Link	Booth (1958)
	T. phaeostroma (Dur. & Mont.) Booth	
	= Oedemium minus (Link) Hughes	Booth (1958)
2.3.1.	Thecotheus cinereus (Cr. & Cr.) Chen.	
	= Sporothrix vel aff.	Conway (1975)
	T. pelletieri (Cr. & Cr.) Boudier	
	= Rhinocladiella sp.	Conway (1975)
2.3.1.	Thermoascus crustaceus (Apin. & Ches.) Stolk	
	= Paecilomyces crustaceus Apin. & Stolk	Stolk (1965), Samson (1974), Udagawa et al. (1973)
2.3.1.	T. thermophilus (Sopp) Arx	
	= [?] Polypaecilum sp.	Arx (1974)
	Therrya pini (Alb. & Schw. ex Fr.) Höhn.	
	= Colpomella pini Höhn.	C.B.S. catalogue
2.3.1.	Thielavia novoguineensis Udagawa & Horie	
	= Chrysosporium sp.	Udagawa & Horie (1972)
2.3.1.	T. polygonoperda Mats.	
	= Trichosporiella vel aff. (cf. Beniowskia fide DiCosmo)	Matsushima (1975)
2.3.1.	T. sepedonium Emmons	
	= Chrysosporium sp.	Tubaki (1955), Barron (1968),
	= Sepedonium sp.	Matsushima (1971), Arx (1974)
2.3.1.	T. setosa Dade	
	= Chrysosporium sp.	Booth (1961), Horie & Udagawa (1973)
2.3.1.	T. terrestris (Apinis) Mall. & Cain	
	= Acremonium alabamense G. Morgan-Jones	Samson et al. (1977)
2.3.1.	Thuemenella britannica Rifai & Webster	
	= Trichoderma sp.	Rifai & Webster (1965)
2.3.1.	Thyridaria sp.	
	= Diplodia sp.	Bancroft (1911), Tunstall (1929)
2.2.2.	Thyronectria berolinensis (Sacc.) Seaver	
	= [?] Dendrodochium vel aff.	Booth (1959)
	= ascospores with phialidic apertures	
2.3.1.	T. balsamea (Cooke & Peck) Seeler	
	= ascospores with phialidic apertures	
	= unnamed phialidic coelomycete	Booth (1959)
2.3.1.	T. lamyi (Desm.) Seeler	
	= ascospores with phialidic apertures	
	= unnamed phialidic coelomycete	Booth (1959)
	T. pseudotricha (Schw.) Seeler	
	= Stilbella cinnabarina (Mont.) Wollenw.	Booth (1959)
2.3.1.	Torrubiella alba Petch	
	= Verticillium aranearum (Petch) Gams	Gams (1971)

2.3.1.	T. arachnophila (Johnst.) Mains var. pleiopus Mains	
	= Gibellula pleiopus (Vuill.) Mains	Mains (1950)
2.3.1.	T. hemipterigena Petch	
	= Verticillium hemipterigena Petch	Gams (1971)
	Torrubiella spp.	
	= Hirsutella spp.	Morris (1963)
2.3.1.	Triangularia angulospora Cain & Farr.	
	= [?] Phialophora sp.	Cain & Farrow (1956)
2.3.1.	T. backusii Huang	
	= Phialophora sp.	Huang (1975)
2.3.1.	T. bambusae (van Beyma) Boed.	
	= [?] Phialophora sp.	Cain & Farrow (1956)
	Trichocoma paradoxa Jungh.	
	= Penicillium sp.: (after 52 months also produces Acremonium vel aff. besides Penicillium sp.)	Malloch & Cain (1952)
2.3.1.	Trichophaea abundans (Karst.) Boud.	
	= Dichobotrys abundans Henneb.	Hennebert (1973)
2.3.1.	T. brunnea (Alb. & Schw.) Batra in Batra & Batra	
	= Dichobotrys sp.	Whitney & Parmeter (1964)
2.3.1.	T. bullata Kanouse	
	= Rhizoctonia hiemalis Saksena & Vaartaja	Whitney & Parmeter (1964)
2.3.1.	T. confusa (Cke.) Berth.	
	= 'aleuriospores' vel aff.	Berthet (1966)
2.3.1.	T. minuta (Cain) Korf in Henneb.	
	= Dichobotrys sessilispora Henneb.	Hennebert (1973)
2.3.1.	T. saccata (Evans) Korf in Henneb.	
	= Dichobotrys parvispora Henneb.	Hennebert (1973)
	Trichophaea sp.	
	= Botrytis vel aff.	Tubaki (1958), Paden (1972), Korf (1973)
2.3.1.	Trichoscyphella calycina (Schüm. ex Fr.) Nannf.	
	= [?] Cytospora sp.	Berthet (1964)
2.3.1.	T. gallica (Karst. & Har.) Berthet var. robusta Grelet.	
	= [?] Cytospora sp.	Berthet (1964)
	Trichosphaerella arecae (Syd.) E. Müller	
	= Acremonium sp.	Gams (1971)
	Tripterospora erostrata (Griff.) Cain	
	= [?] Acremonium sp.	
	or = [?] Phialophora sp.	Cain (1971)
2.2.2.	Trochila craterium Fr.	
	1.1. = [?] Ceuthospora hederae Gr.	
	= [?] Cryptocline paradoxa (de Not.) Arx	Grove (1935), Arx (1957)
2.1.	T. laurocerasi Fr.	
	= [?] Ceuthospora laurocerasi Gr.	
	= [?] Cryptocline phacidiella (Gr.) Arx	Grove (1935)
	T. populorum Desm.	
	= Marssonina populi-nigrae Kleb.	Grove (1937), Arx (1957)
2.2.2.	Tympanis alnea Pers. ex Fr.	
	= Sirodothis inversa (Fr.) Sutt. & Funk	Sutton & Funk (1975)
2.2.2.	T. amelanchieris Groves	
	= Sirodothis vel aff.	
	or = Pragmopycnis vel aff.	Groves (1952)
2.2.2.	T. confusa Nyl.	
	= Sirodothis vel aff.	
	or = Pragmopycnis vel aff.	Groves (1952)
2.2.2.	T. conspersa Fr.	
	= Sirodothis vel aff.	
	or = Pragmopycnis vel aff.	Groves (1952)

	T. fasciculata Schw.	
	= Sirodothis vel aff.	
	or = Pragmopycnis vel aff.	Groves (1952)
2.2.2.	T. hypopodia Nyl.	
	= Sirodothis vel aff.	
	or = Pragmopycnis vel aff.	Groves (1952)
2.2.2.	T. laricina (Fckl.) Sacc.	
	= Sirodothis vel aff.	
	or = Pragmopycnis vel aff.	Groves (1952)
2.2.2.	T. ligustri Tul.	
	= Sirodothis columnaris (Wallr.) Sutt. & Funk	Sutton & Funk (1975)
2.2.2.	T. malicola Groves	
	= Sirodothis vel aff.	
	or = Pragmopycnis vel aff.	Groves (1952)
2.2.2.	T. mutata (Fckl.) Rehm	
	= Sirodothis vel aff.	Groves (1952)
	T. neopithya Ouell. & Piroz.	
	= Sirodothis vel aff.	
	or = Pragmopycnis vel aff.	Groves (1952)
2.2.2.	T. oxydendri Ell. & Ev.	
	= Sirodothis vel aff.	
	or = Pragmopycnis vel aff.	Groves (1952)
2.2.2.	T. piceae Groves	
	= Sirodothis vel aff.	
	or = Pragmopycnis vel aff.	Groves (1952)
	T. prunicola Groves	
	= Sirodothis vel aff.	Groves (1952)
2.2.2.	T. rhabdospora B. & C.	
	= Sirodothis vel aff.	
	or = Pragmopycnis vel aff.	Groves (1952)
	T. rhoina Groves	
	= Sirodothis vel aff.	
	or = Pragmopycnis vel aff.	Groves (1952)
	T. salicina Groves	
	= Sirodothis vel aff.	Groves (1952)
	T. saligna Tode ex Fr.	
	= Sirodothis saligna (Höhn.) Sutt. & Funk	Sutton & Funk (1975)
	T. spermatiospora (Nyl.) Nyl	
	= Sirodothis populnea (Thüm.) Sutt. & Funk	Sutton & Funk (1975)
	T. truncatula (Pers. ex Fr.) Rehm	
	= Sirodothis vel aff.	
	or = Pragmopycnis vel aff.	Groves (1952)
2.2.2.	T. tsugae Groves	
	= Sirodothis vel aff.	
	or = Pragmopycnis vel aff.	Groves (1952)
2.3.1.	Uncinocarpus reesii Sig. & Carm.	
	= Malbranchea sp.	Sigler & Carmichael (1976)
2.2.4.	Uncinula bicornis Lév.	
	= Oidium aceris Rab.	Mukerji (1968)
2.2.4.	U. brachystegiae (Doidge) Piroz.	
	= Oidium sp.	Deighton & Pirozynski (1965)
2.2.4.	U. combreticola Doidge	
	= Oidium sp.	Deighton & Pirozynski (1965)
2.2.4.	U. crotonis Piroz.	
	= Oidium sp.	Deighton & Pirozynski (1965)
2.2.4.	U. incrassata Salmon var. afrormosiae Piroz.	
	= Oidium sp.	Deighton & Pirozynski (1965)
2.2.4.	U. necator (Schw.) Bur. in Ell. & Ev.	
	= Oidium sp.	Kapoor (1967)
1.1.	Unguiculariopsis sp.	
	= unnamed coelomycete (pycnidial)	Korf (1973)

2.3.1.	Urnula craterium (Schw.) Fr.	
	2.3.1. = Conoplea globosa (Schw.) Hughes	
	2.3.1. = Strumella coryneoides Sacc. & Wint.	
	2.3.1. = Verticicladium sp.	Davidson (1950), Paden (1972)
2.2.1.	Urosporella magnoliae (Ell. & Ev.) Barr	
	= unnamed coelomycete (pycnidial)	Ellis & Everhart (1897), Barr (1966)
	Valdensinia heterodoxa	
	= Valdensia sp.	Ainsworth et al. (1971)
1.1.	Valsa abietis (Fr.) Fr.	
	= Cytospora abietis Sacc.	Grove (1935)
1.1.	V. ambiens (Pers. ex Fr.) Fr.	
	= Cytospora ambiens Sacc. (cf. C. oxyancanthae Rab. and C. carphosperma Fr.)	Grove (1935)
1.1.	V. aquifolii Nits.	
	= Cytospora ilicina Sacc.	Grove (1935)
1.1.	V. betulina Nits.	
	= Cytospora ambiens Sacc.	Grove (1935)
2.2.2.	V. ceratophora Tul.	
	= Cytospora ceratophora Sacc.	Grove (1935)
1.1.	V. cincta Fr.	
	= Cytospora cincta Sacc.	Grove (1935)
1.1.	V. curreyi Nits.	
	= Cytospora curreyi Sacc.	Grove (1935)
1.1.	V. cypri Tul.	
	= Cytospora pruinosa Sacc.	Grove (1935)
1.1.	V. eunomia Nits.	
	= Cytosporina millipunctata Sacc.	Grove (1935)
1.1.	V. fallax Nits.	
	= Cytospora corni Westd.	Grove (1935)
2.2.1.	V. friesii (Duby) Fckl.	
	= Cytospora friesii Sacc.	Grove (1935), Shaw (1973)
1.1.	V. fuckelii Nits.	
	= Cytospora fuckelii Sacc.	Grove (1935)
1.1.	V. germanica Nits.	
	= Cytospora germanica Sacc.	Grove (1937)
1.1.	V. horrida Nits.	
	= Cytospora horrida Sacc.	Grove (1935)
1.1.	V. intermedia Nits.	
	= Cytospora intermedia Sacc.	Grove (1935)
1.1.	V. kunzei Nits.	
	= Cytospora kunzei Sacc.	Grove (1935)
1.1.	V. laburni All.	
	= Cytospora laburni Peyr.	Grove (1935)
1.1.	V. laurocerasi Tul.	
	= Cytospora laurocerasi Fckl.	Grove (1935)
2.2.2.	V. leucostoma (Pers. ex Fr.) Fr.	
	= Cytospora leucostoma (Pers.) Sacc.	Grove (1935), Shaw (1973)
1.1.	V. microstoma Nits.	
	= Cytospora microstoma Sacc.	Grove (1935)
1.1.	V. nivea (Pers. ex Fr.) Fr.	
	= Cytospora nivea Sacc.	Grove (1935), Shaw (1973)
1.1.	V. olivacea Fckl.	
	= [?] Cytospora lonicerae Gr.	Grove (1935)
1.1.	V. pini (Alb. & Schw. ex Fr.) Fr.	
	= Cytospora pini Desm	Grove (1935), Shaw (1973)
1.1.	V. populina Fckl.	
	= Cytospora populina Rabenh.	Grove (1935)
1.1.	V. rhodophila B. & Br.	
	= Cytospora rhodophila Sacc.	Grove (1935)
1.1.	V. rosarum de Not.	
	= "Cytospora rosarum Grev. in Bail."	Grove (1935)
1.1.	V. salicina Fr.	
	= Cytospora salicis Rab.	Grove (1935), Shaw (1973)

1.1.	V. schweinitzii Nits.	
	= Cytospora capreae Fckl.	Grove (1935)
1.1.	V. sordida Nits.	
	= Cytospora chrysosperma Pers. ex Fr.	Grove (1935), Shaw (1973)
1.1.	V. syringae Nits.	
	= Cytospora syringae Sacc.	Grove (1935)
1.1.	V. taxi Fckl.	
	= Cytospora taxi Sacc.	Grove (1935)
1.1.	V. translucens (de Not.) Ces. & de Not.	
	= Cytospora translucens Sacc.	Grove (1935), Sacc. (1973)
1.1.	V. viburni Fckl.	
	= Cytospora lantanae Bres.	Grove (1935)
1.1.	Valsella clypeata Fckl.	
	= Cytospora clypeata Sacc.	Grove (1935)
1.1.	V. fertilis Sacc.	
	= Cytospora fertilis Sacc.	Grove (1935)
1.1.	V. myricae Bres.	
	= Cytospora myricae-gales Bres.	Grove (1935)
	Valseutypella tristicha	
	= Cytospora sp.	Hubbes (1960), Müller & Arx (1973)
	Valsonectria reticulata Loeff. & Müll.	
	= Sporothrix sp.	Loeffler & Müller (1961)
	Wallrothiella subiculosa Höhn.	
	= Acremonium sp.	
	= Gliomastix protea (Sacc.) Ver. & Cast.	Gams (1971)
2.3.1.	Waltonia pinicola Saho apud Saho & Takah.	
	= unnamed pycnidial coelomycete	Saho & Takahashi (1967)
2.3.1.	Warcupiella spinulosa (Warcup) Subram.	
	= Aspergillus spinulosus Warcup in Raper & Fennell	Arx (1974)
	Xanthothecium peruvianum Arx & Sams.	
	= "Chrysosporium (Trichophyton)-like"	Arx & Samson (1973)
	Xeromyces bispora Fraser	
	= Fraseriella bispora Cif. & Corte	Kendrick & Carmichael (1973)
2.3.1.	Xylogone sphaerospora Arx & Nilss.	
	= Bahusakala sp.	Fennell (1973), Arx (1974)
2.2.2.	Xylogramma sp. (Durella sp. q.v.)	
	= Cystotricha sp.	Dennis (1956)
2.3.1.	Xylosphaera furcata (Fr.) Dennis	
	= Nodulisporium vel aff.	
	= Padixonia vel aff.	Dixon (1965), Subramanian (1972)
2.3.1.	Xynophila mephitalis Mall. & Cain	
	= 'arthrospores'	Malloch & Cain (1971)
	Zendera sp.	
	= Geotrichum sp.	Carmichael, Kendrick & Conners (1979)
1.1.	Zignoella pulviscula Curr.	
	= Aposphaeria pulviscula Sacc.	Grove (1935)
1.1.	Zignoella sp.	
	= Aposphaeria agminalis Sacc.	Grove (1935)
	Zopfiella latipes (Lundq.) Mall. & Cain	
	= Humicola sp.	Malloch & Cain (1971)
	Zopfiella marina Furuya & Udagawa	
	= Chrysosporium sp.	Furuya & Udagawa (1975)
2.3.1.	Z. pilifera Udag. & Fur.	
	= Chrysosporium vel aff.	Udagawa & Furuya (1972)
2.3.1.	Z. pleuropora Mall. & Cain	
	= [?] Acremonium vel aff.	
	= [?] Phialophora vel aff.	Malloch & Cain (1971)

TELEOMORPH-ANAMORPH CONNECTIONS

ALPHABETICALLY BY UNITUNICATE ASCOMYCETE ORDER AND FAMILY

INDICATING NUMBER OF CONNECTIONS IN EACH ANAMORPH GENUS

Clavicipitales

Clavicipitaceae

Acrospermum Tode ex Fr.
= Dactylaria (1)
= Virgariella vel aff. (1)

Balansia Speg.
= Ephelis (2)

Claviceps Tul.
= Sclerotium (1)
= Sphacelia (2)

Cordyceps (Fr.) Link
= Acremonium (1)
= Akanthomyces (1)
= Gibellula (1)
= Hirsutella (3)
= Hymenostilbe (2)
= Isaria (1)
= Paecilomyces (1)
= Sphacelia (1)
= Verticillium (1)

Epichloë Fr.
= Sphacelia (1)

Hypocrella Sacc.
= Aschersonia (7)

Ophiocordyceps Petch
= Hirsutella (1)

Torrubiella Boud.
= Gibellula (2)
= Verticillium (2)

Coronophorales

Coronophoraceae

Acanthonitschkea Speg.
= Acremonium (1)

Parkerella Funk
= Cladorrhinum vel aff.
or Cyphellophora vel aff. (1)

Thaxteria Sacc. (see Müller & Arx (1973), Luttrell (1973))
= Oedemium (2)

Endomycetales

Ascoideaceae

Botryoascus Arx
= Raffaelea vel aff. (1)

Dipodascus Langer
= [?] Trichosporon (1)

Endomycetaceae

Debaryomyces Klöcker
= Torulopsis (1)

Endomyces Rees
= Geotrichum (2)

Saccharomycetaceae

Dekkera van der Walt
= Brettanomyces (2)

Endomycopsis Stelling-Dekker
= Candida (1)

Hanseniaspora Zikes
= Kloeckera (1)

Hansenula Syd.
= Candida (1)
Lipomyces Lodder & Kreger van Rij.
= Cryptococcus (1)
Pichia Hans.
= Candida (1)
= unnamed blastic hyphomycete (1)
Saccharomyces Meyen emend. Rees.
= Candida sp. (1) cf. Torulopsis

Spermophthoraceae
Metschnikowia Kamien.
= Candida (2)
Nematospora Pegl.
= Candida (1) cf. Torulopsis

Erysiphales
Erysiphaceae
Erysiphe Hedw. ex Fr.
= Oidium (7)
Leveillula Arn.
= Oidiopsis (2)
Microsphaera Lév.
= Oidium (1)
Phyllactinia Lév.
= Oidium (1)
= Ovulariopsis (1)
Pleochaeta Sacc. & Speg.
= Ovulariopsis (2)
Podosphaera Kunze ex Lév.
= Oidium (4)
Sphaerotheca Lév.
= Oidium (3)
Uncinula Lév.
= Oidium (6)

Eurotiales
Amorphothecaceae
Amorphotheca Parberry
= Sorocybe (1)
= Hormoconis (1)
Thermoascus Miehe
= Paecilomyces (1)
= Polypaecilum (1)

Cephalothecaceae
Cephalotheca Fuckel
= Acremonium vel aff. (1)
Nigrosabulum Mall. & Cain
= Acremonium (1)

Eurotiaceae
Albertiniella Kirschst.
= Acremonium (1)
Ascorhiza Lech.-Trnka.
= terminal chlamydospores (1)
Cephalotheca Fuckel
= Paecilomyces (1)
= Tritirachium (1)
Diplostephanus Lang.
= Sterigmatocystis sp. (1)
Fragosphaeria Shear (= Cephalotheca Fuckel fide Chesters)
= Sporothrix (2)
Heleococcum Jorg.
= Acremonium (1)

Levispora Rout.
= Acremonium (1)

Roumegueriella Speg.
= Gliocladium (1)

Sagenoma Stolk & Orr
= Acremonium (1)

Xeromyces Fraser
= Fraseriella (1)

Gymnoascaceae

Ajellomyces McDonough & Lewis (=Arthroderma fide Carmichael)
= Chrysosporium (1)

Apinisia LaTouche
= Chrysosporium (2)

Arachniotus Schroeter
= Acladium vel aff. (1)
= Chrysosporium (1)
= Geotrichum vel aff. (1)
= Oidiodendron (1)
= Scopulariopsis (1)
= unnamed arthric hyphomycete (2)

Arachnotheca Arx
= Arthrographis (1)

Arthroderma Berk.
= Chrysosporium (2)
= Keratinomyces (1)
= Trichophyton (7)
= chlamydospores (1)

Auxarthron Orr & Kuehn
= Malbranchea (1)

Byssoascus Arx
= Oidiodendron (1)

Ctenomyces Eidam
= Chrysosporium (1)

Eleutherascus Arx
= [?] Nodulisporium (1)

Emmonsiella Benj.
= Chrysosporium (1)
= Histoplasma (1)

Gymnoascus Baranetzky
= Chrysosporium vel aff. (1)

Gymnoascella
= Malbranchea (1)

Gymnoascoideus
= Malbranchea (1)

Lilliputia Boud. & Pat.
= Gliocladium (1)
= Phialocephala (1)

Macronodus
= Malbranchea (1)

Myxotrichum Kunze
= Malbranchea (2)
= Oidiodendron (2)

Nannizzia Stock
= Microsporum (9)

Plunkettomyces
= Malbranchea (1)

Pseudogymnoascus Raillo
= Geomyces (1)

Rollandina Apinis
= Chrysosporium (1)

Uncinocarpus Sig. & Carm.
= Malbranchea (1)

[?] Zendera
= Chrysosporium (1)

Monascaceae	
Monascus van Tiegh.	= Basipetospora (1)
Onygenaceae	
Anixiopsis Hansen	= Chrysosporium (1)
Aphanoascus Zuk.	= Chrysosporium (5) = Paecilomyces (1)
Ascocalvatia Cain	= unnamed arthric hyphomycete (1)
Keratinophyton Randhawa & Sandhu	= Trichophyton (1)
Neoxenophila Apinis & Clark	= Chrysosporium (1)
Onygena Pers. ex Fr.	= Sporendonema (1) = unnamed hyphomycete (2)
[?] Xanthothecium Arx & Samson	= Chrysosporium vel aff. (1)
Xylogone Arx & Nilsson	= Bahusakala (1)
Xynophila Malloch & Cain	= arthric (1)
Pseudeurotiaceae	
Cryptendoxyla Malloch & Cain	= Chalara (1)
Emericellopsis van Beyma	= Acremonium (8) = Stilbella (1)
[?] Ephemeroascus van Emden	= Verticillium (1)
Hapsidospora Malloch & Cain	= Acremonium (1)
Mycoarachis Malloch & Cain	= Acremonium (1)
Pseudeurotium van Beyma	= Geotrichum (1) = Sporothrix (3)
Thermoascaceae	
Dactylomyces Sopp	= Paecilomyces (2)
Trichocomaceae	
Byssochlamys Westl.	= Paecilomyces (4)
Chaetosartorya Subram.	= Aspergillus (3)
Dichlaena Dur. & Mont.	= Aspergillus
Dichotomomyces Saito ex Scott	= Polypaecilum (1)
Edyuillia Subram.	= Aspergillus (1)
Emericella Berk. & Br. in Berk.	= Aspergillus (13)
Eupenicillium Ludwig	= Penicillium (42)
Eurotium Link ex Fr.	= Aspergillus (17)
Fennellia Wiley & Simmons	= Aspergillus (1)
Gymnoeurotium Malloch & Cain	= Aspergillus (1)

Hamigera Stolk & Samson
= Penicillium (2)

Harpezomyces Malloch & Cain
= Aspergillus (2)

Hemicarpenteles Sarbhoy & Elphick
= Aspergillus (2)

Neosartorya Malloch & Cain
= Aspergillus (10)

Penicilliopsis Ghosh, Orr & Kuehn
= Penicillium vel aff. (1)

Petromyces Malloch & Cain
= Aspergillus (1)

Sclerocleista Subram.
= Aspergillus (1)

Talaromyces Benjamin
= Paecilomyces (1)
= Penicillium (17)

Trichocoma Jungh.
= Penicillium (1)
= Acremonium (1)

Warcupiella Subram.
= Aspergillus (1)

Eurotiales [?]

Sphaeriales [?]

Echinopodospora Jong & Davis
= Chrysosporium (1)

Thielavia Zopf
= Acremonium (1)
= Chrysosporium (3)
= Sepedonium (1)
= Trichosporiella (1)
= unnamed phialidic hyphomycete (1)

Eurotiales [?]

Xeromyces L. Fraser
= Fraseriella (1)

Helotiales

Ascocorticiaceae

Ascocorticium Bref.
= Acrodontium (1)

[?] Calloriopsis Syd.
= Eriomycopsis (1)

Dermateaceae

Atropellis Zeller & Good.
= Fuckelia (1)
= Neofuckelia (2)

Belonopsis (Sacc.) Rehm
= Cystodendron (2)

Blumeriella Arx
= Phloeosporella (2)

Callorina Korf
= Cylindrocolla (1)

Dermea Fr.
= Cornicularíella (2)
= Foveostroma (2)
= Gelatinosporium (1)
= "Micropera" (3)

Diplocarpon Wolf
= Actinonema (1)
= [?] Bostrichonema (1)
= Entomosporium (2)
= "Marssonia" (2)
= Septogloeum (1)

Discohainesia Nannf.
= Hainesia (1)
= Pilidium (1)

Drepanopeziza (Kleb.) Höhn.
= Gloeosporidiella (1)
= "Marssonia" (2)
= Marssonina (4)
= Monostichella (1)

Encoeliopsis Nannf.
= Brunchorstia (1)
= Diplodina (1)

Fabraea Sacc.
= Septoria (1)

Godroniopsis Dichl. & Cash
= "Micropera" (1)

Habrostictis Fuckel
= Cryptosporiopsis (1)

Higginsia Nannf.
= "Cylindrosporium" (3)
= Hainesia (1)
= Phloeosporella (1)

Leptotrochila Karst.
= Sporonema (7)

Merostictis Clem.
= Acremonium (1)

Mollisia (Fr.) Karst.
= Anguillospora (1)
= Phialophora (2)

Ocellaria (Tul.) Karst.
= Cryptosporium (1)
cf. Myxosporium

Pezicula Tul.
= Ascoconidium (1)
= Catinula (1)
= Cryptosporiopsis (11)
= Myxosporium (6)
= Phlyctaena (1)
= Sphaerographium (1)
= Sphaeronaema (2)
= unnamed coelomycete (2)

Propolis (Fr.) Fr.
= Pseudopatellina (1)

Pseudopeziza Fuckel
= Cylindrosporium (1)
= Gloeosporidiella (2)
= Gloeosporiella (1)
= Marssonina (1)
= Sporonema (2)
= Stagonospora (2)

Pyrenopeziza Fuckel
= Marssonina (1)
= Phialophora (1)
= Phoma (1)

Tapesia (Pers. ex Fr.) Fuckel
= Cystodendron (4)

Trochila Fr.
= Ceuthospora (2)
= Cryptocline (2)
= Marssonina (1)

Waltonia Saho apud Saho & Takah.
= unnamed coelomycete (1)
(cf. Corniculariella)

Hemiphacidiaceae

Rhabdocline Syd. apud Syd. & Petr.
= Rhabdogloeum (2)

Sarcotrochila Höhn.
= Kabatiella (1)

Hyaloscyphaceae
Calycellina Höhn.
= Chaetochalara (1)
Dasyscypha (Fr.) Fuckel
= Cytospora (1)
Hyaloscypha Boud.
= Chaetochalara (1)
= Clathrosphaerina (1)
= Haplographium (1)
Lachnellula Karst.
= [?] Naemospora (14)
Trichoscyphella Nannf.
= Cytospora (1)
Unguiculariopsis Rehm
= unnamed coelomycete (pycnidial) (1)
Leotiaceae
Ascocalyx Naumov
= Bothrodiscus (2)
= Brunchorstia (1)
Ascocoryne Groves
= Coryne (1)
Bisporella Sacc.
= Cystodendron (1)
Cenangium Fr.
= Brunchorstia (1)
= Chondroplea (1)
Chlorociboria Seaver ex Ramamurthi, Korf & Batra
= Dothiorina (2)
Claussenomyces Kirschst.
= Dendrostilbella (1)
= Sirodothis or Pragmopycnis vel aff. (1)
= ascospores bud in the ascus (1)
Crumenulopsis Groves
= Digitosporium (2)
Durandiella Seaver
= Corniculariella (2)
Godronia Moug. & Lév. apud Moug.
= Chondropodiella (1)
= [?] Dothichiza (1)
= Fuckelia (1)
= Fusicoccum (1)
= Phlyctaena (2)
= Septomyxa (1)
= Topospora (5)
= unnamed coelomycetes (10)
"Helotium Pers. ex Gray"
= Cylindrocolla (1)
= Stilbella (1)
Heterosphaeria Grev.
= Heteropatella (3)
Holwaya Sacc.
= Crinula (1)
Hymenoscyphus Gray
= Idriella (1)
= Varicosporium (1)
Ombrophila Fr.
= Acleistia (1)
Pestalopezia Seaver
= Pestalotia (1)
= [?] Seiridium (1)
Pezizella Fuckel
= Hainesia (1) cf. Discohainesia sp.
= Leptothyrium (1)
= Sclerotiopsis (1)

Phialea (Fr. ex Fr.) Gill
= Endoconidium (1)

Pragmopora Massalongo
= Pragmopycnis (1)

Rhizocalyx Petr.
= Rhizothyrium (1)

Sageria Funk
= Ascoconidium (1)

Scleroderris (Fr.) de Not.
= Brunchorstia (1)

Staminaria Fuckel
= Titaeospora (3)

Strossmayeria Schulz.
= [?] Bipolaris vel aff. (1)
= Helminthosporium vel aff. (1)

Tympanis Tode ex Fr.
= Pragmopycnis vel aff. or Sirodothis vel aff. (14)
= Sirodothis (6)

Xylogramma Wallr.
= Cystotricha (1)

Orbiliaceae

Orbilia Fr.
= Dicranidion (2)

Orbiliella Kirscht.
= [?] Trichothecium (1)

Sclerotiniaceae

Botryotinia Whetz.
= Amphobotrys (1)
= Botrytis (4)

Ciboria Fuckel
= Botrytis vel aff. (1)
= Myrioconium (1)

Ciborina Whetz.
= Sclerotium (1)

Gloeotinia Wilson, Noble & Gray
= Endoconidium (1)

Monilinia Honey
= Monilia (7)

Myriosclerotinia Buchw.
= Myrioconium (1)

Ovulinia Weiss
= Ovulitis (1)

Phaeosclerotinia Hori
= Monilia (1)

Pycnopeziza White & Whetz.
= Acarosporium (2)

Rutstroemia Karst.
= Myrioconium sp. (3)
= Phialophora vel aff. (2)

Sclerotinia Fuckel
= Botrytis (11)
= Monilia (3)
= Myrioconium (3)
= Rhacodiella (1)
= Sclerotium (1)

Seaverina Whetz.
= Verrucobotrys (1)

Septotinia Whetz. ex Groves & Elliott
= Septotis (2)

Stromatinia (Boud.) Boud.
= Sclerotium (3)

Streptotinia Whetz.
= Streptobotrys (2)

Valdensinia Peyron.
= Valdensia (1)

[?] Symphyosirinia E.A. Ellis
= Symphyosira (1)

Hypocreales

Hypocreaceae

Calonectria de Not.
= Acremonium (1)
= Cylindrocarpon (1)
= Cylindrocladium (7)
= Fusarium (2)

Gibberella Sacc.
= Fusarium (13)
= Stagonostroma

Hypocrea Fr.
= Acremonium (2)
= Fusarium (1)
= Gliocladium (2)
= [?] Penicillium (1)
= Trichoderma (13)

Hypocrella Sacc.
= Aschersonia (7)

Hypocreopsis Karst.
= Stromatocrea (1)

Micronectriella Höhn.
= Fusarium (3)

Mycocitrus Moeller
= Acremonium (1)

Myrmaeciella Lindau
= Patellina (1)

Nectria Fr.
= Acremonium (21)
= Aschersonia (1)
= Calostilbella (1)
= Cylindrocarpon (13)
= Dendrodochium (4)
= Flagellospora (1)
= Fusarium (14)
= Gliocladium (6)
= [?] Graphium (1)
= Heliscus (1)
= Kutilakesopsis (1)
= Myrothecium (1)
= [?] "Sphaeropsis" (2)
= Stilbella (3)
= Stromatographium (1)
= Tubercularia (1)
= Verticillium (3)
= Volutella (1)
= Zythiostroma (1)

Nectriella Nits.
= Illosporium (1)

Nectriopsis Maire
= Acremonium (2)
= Cylindrocarpon (1)
= Fusarium (1)
= chlamydospores (1)

Neocosmospora E.F. Smith
= Acremonium vel aff. (2)
= Fusarium (1)

Ophionectria Sacc.
= Antipodium (1)
= Helicomyces (1)
= Helicosporium (1)
= Peziotrichum (1)

Peloronectriella Doi
= Acremonium (1)

Pleonectria Sacc.
= Dendrochium (1)

Podocrea (Sacc.) Lindau
= Verticillium (1)

Podostroma Karst.
= Trichoderma vel aff. (4)
= Verticillium vel aff. (1)

Pseudonectria Seaver
= Sesquicillium (1)
= Tilachlidium (1)
= Volutella (2)

Roumegueriella Speg.
= Gliocladium (1)

[?] Hypocreaceae
Schizoparme Shear
= [?] Coniella (1)

Scoleconectria Stev. & Manter
= [?] Verticillium (1)
= Zythiostroma (1)

Sphaerostilbe Tul.
= Atractium (2)

Thuemenella Penz. & Sacc.
= Trichoderma (1)

Thyronectria Sacc.
= Dendrochium (1)
= Stilbella (1)
= ascospores with phialidic apertures (3)
= unnamed phialidic coelomycete (2)

Valsonectria Speg.
= Sporothrix (1)

Hypomycetaceae
Apiocrea Syd.
= Sepedonium (2)

Hypomyces (Fr.) Tul.
= Blastotrichum (1)
= Cladobotryum (12)
= Dactylaria (2)
= Dactylium (2)
= Fusarium (3)
= Gliocladium (4)
= Moeszia (3)
= Mycogone (1)
= [?] Penicillium (1)
= [?] Polyscytalum (1)
= Sepedonium (2)
= Sibirina (2)
= Stephanoma (1)
= Trichothecium (8)
= Verticillium (9)

Peckiella (Sacc.) Sacc.
= Acremonium (8)
= Sepedonium (8)

Pyxidiophora Bref. & Tavel
= Chalara vel aff. (1)
= Paecilomyces (1)

[?] Byssostilbe Petch
= Stilbella (1)

[?] Calostilbe Sacc. & Syd.
= Calostilbella (2)

Microascales
Microascaceae
Kernia Nieuwl.
= [?] Graphium (1)
= Scopulariopsis (4)
Microascus Zukal
= Dematophora (1)
= Phialophora (1)
= Scopulariopsis (13)
= Wardomyces (1)
= Wardomycopsis (2)
Petriella Curzi
= Graphium (3)
= Scopulariopsis (1)
Petriellidium Malloch
= Graphium (1)
= "Scedosporium" (2)
Ophiostomataceae
Ceratocystiopsis Upad. & Kendr.
= Hyalorhinocladiella (1)
= Sporothrix (1)
Ceratocystis Ellis & Halst. emend. Bakshi
= Acremonium (2)
= Chalara (8)
= Graphilbum (2)
= Graphium (7)
= Hyalodendron (3)
= Hyalopesotum (1)
= Hyalorhinocladiella (8)
= Leptographium (8)
= Pachnodium (1)
= Pesotum (6)
= Phialocephala (1)
= Phialographium (3)
= Sporothrix (5)
= Trichosporon [?] (1)
= Verticicladiella (11)
= Yeast-like (3)
= unnamed blastic-sympodial hyphomycete (4)
Europhium A.K. Parker
= Leptographium (1)
= Verticicladiella (3)
Ophiostoma Syd.
= [?] Acrodontium (1)
= Graphium (2)
= Sporothrix (11)
Sphaeronaemella Karst.
= Gabarnaudia (2)

Ostropales
Stictidaceae
Biostictis Petr.
= Cylindrocarpon or Fusidium (1)
= Rhinocladiella (1)
Stictis Pers. ex Gray
= Fusidium (1)

Pezizales
Aleuriaceae
Caloscypha Boud.
= Geniculodendron (1)

Ascobolaceae
- Ascobolus Pers. ex Hook
  - = Monilia (2)
  - = Papulaspora (1)
  - = Stemphylium vel aff. (1)
  - = "oidia" (1)
- [?] Cleistoiodophanus
  - = Oedocephalum (1)
- Iodophanus Korf apud Kimbr. & Korf
  - = Oedocephalum (1)
- Thecotheus Boud.
  - = Rhinocladiella (1)
  - = Sporothrix vel aff. (1)

Morchellaceae
- Morchella St. Amans
  - = Costantinella (2)

Pezizaceae
- "Galactinia (Cke.) Boud."
  - = Oedocephalum (5)
- Peziza L. ex St. Amans
  - = Botrytis vel aff. (2)
  - = Chromelosporium (5)
  - = Hainesia (1)
  - = [?] Phialophora (1)
  - = Oedocephalum (8)
  - = "aleuriospores" (2)
  - = unnamed holoblastic hyphomycete (1)

Pyronemataceae
- Anthracobia Boud.
  - = [?] Scytalidium (1)
- Ascophanus Boud.
  - = Oedocephalum (1)
- Geopyxis (Pers.) Sacc.
  - = Hansfordia (2)
- Miladina (Cke.) Svrcek
  - = Actinospora (1)
- Plicaria Fuckel
  - = Acladium (1)
- Pyronema Carus
  - = Oedocephalum (1)
- Tarzetta (Cke.) Lamb
  - = Oedocephalum (1)
- Trichophaea Boud.
  - = Botrytis vel aff. (1)
  - = Dichobotrys (1)
  - = Rhizoctonia (1)
  - = "aleuriospores" vel aff. (1)

Sarcoscyphaceae
- Desmazierella Lib.
  - = Verticicladium (1)
- Korfiella Pant. & Tewari
  - = Conoplea (1)
- Nanoscypha Denison
  - = unnamed hyphomycete (1)
- Phillipsia Berk.
  - = Blastobotrys vel aff. (1)
  - = unnamed sympodial hyphomycete (1)
- Pithya Fuckel
  - = Botrytis vel aff. (1)
- Plectania Fuckel
  - = Conoplea (1)
- Sarcoscypha (Fr.) Boud.
  - = Botrytis vel aff. (1)

Sarcosoma Casp.
= Conoplea (1)
Urnula Fr.
= Conoplea (1)
= Strumella (1)
= Verticicladium (1)

Phacidiales
Cryptomycetaceae
Potebniamyces Smerlis
= Aureobasidium (1)
= Fuckelia (1)
= Hormonema (1)
= Phacidiopycnis (4)
Darkera Whitney, Reid & Piroz.
= Tiarosporella (2)
Phacidiaceae
Ascodichaena Butin (in the Phacidiaceae pro temp. fide DiCosmo)
= Polymorphum (1)
Micraspis Darker
= Periperidium (1)
Phacidium Fr.
= Ceuthospora (11)
Pseudophacidium Karst.
= Ceuthospora (1)
= Myxofusicoccum (3)
Therrya Penzig & Sacc.
= Colpomella (1)
Rhytismataceae
Coccomyces de Not.
= Cylindrosporium (3)
= Leptothyrium (3)
= Schizothyrella (1)
Duplicaria Fuckel
= Melasmia (1)
Hypoderma DC. emend. de Not.
= Leptostroma (2)
= Leptothyrium (3)
= sub Gloeosporium (1)
Hypodermella Tubeuf.
= Leptothyrella (1)
Lophodermium Chev.
= Labrella (1)
= Leptostroma (6)
= Leptostromella (2)
= Leptothyrium (2)
Rhytisma Fr.
= Melasmia (6)

Sphaeriales
Amphisphaerellaceae
Blogiascospora Shoem., Müller & Morgan-Jones
= Seiridium (1)
Amphisphaeriaceae
Apiospora Sacc.
= Arthrinium (1)
= Pteroconium (1)
Amphisphaeria Ces. & de Not.
= Bleptosporium (1)
= Dendryphiopsis (1)
Broomella Sacc.
= Monotrichum (1)
= Pestalotia (4)
Discostroma Clem.
= Seimatosporium (3)
= Sporocadus (3)

Griphosphaeria Höhn.
= Fusarium (1)
= Seimatosporium (1)

Griphosphaerioma Höhn.
= Labridella (1)

Hymenopleella Munk
= Seiridium vel aff. (1)

Hyponectria Sacc.
= Macrophoma (1)

Lepteutypa Petr.
= Adea (1)
= Hyalotiopsis (1)
= Seiridium (1)

Pestalosphaeria Barr
= Pestalotiopsis (1)
(see Leptosphaeria Ces. & de Not.)

Physalospora Niessl
= Arthrinium (1)
= Botryodiplodia (1)
= Colletotrichum (1)
= [?] Diplodia (1)
= Diplodina (1)
= Dothiorella (1)
= Macrophoma (1)
= Myxosporium (1)
= Phoma (2)
= Phyllosticta (1)
= Phyllostictina (1)
= Pirostoma (1)
= Sphaeropsis (1)
= Stagonospora (1)

Pseudoguignardia Gutner
= Arthrinium (1)

Pseudomassaria Jacz.
= Beltraniella (1)

Urosporella Atk.
= unnamed coelomycete (pycnidial) (1)

Diaporthaceae

Aporhytisma Höhn. (= Diaporthopsis fide Arx and Müller)
= Apomelasmia (1)

Apiognomonia Höhn.
= Colletotrichum (1)
or Discula (1)
or Sporonema (1)

Apioporthe Höhn.
= Phomopsis (1)

Cryptodiaporthe Petr.
= Chondroplea (1)
= Discella (5)
= Hendersonula (1)
= "Malacostroma" (1)
= Neobarclaya (1)
= Phomopsis (1)

Cryptospora Tul.
= Cryptosporium (2)

Cryptosporella Sacc.
= [?] Cytosporina (1)
= Cryptosporium (3)

Diaporthe Nits.
= Cryptosporium (1)
= Fusicoccum (1)
= Endogloea (1)
= Phomopsis (139)

Diaporthopsis Fabre
= Phomopsis (1)

Endothia Fr.
= Endothiella (2)

Hercospora Fr.
= Rabenhorstia (1)

Gaeumannomyces Arx & Oliver
= Phialophora (1)

Gnomonia Ces. & de Not.
= Cylindrosporella (3)
= Discula (2)
= Marssoniella (1)
= Sesquicillium (1)
= Sporonema (1)
= Zythia (1)

Gnomoniella Sacc.
= Colletotrichum (1)
= Cylindrosporella (1)
= Leptothyrium (1)

Leucostoma (Nits.) Höhn.
= Cytospora (2)

Mazzantia Mont.
= Placosphaeria (1)

Melanconiella Sacc.
= Melanconium (1)
= Myxosporium (2)

Melanconis Tul.
= Cytospora (2)
= Melanconium (19)
= Melanconiopsis (1)
= Myxosporium (1)
= Stilbospora (1)

Melanochaeta Müller, Harr. & Sulmont
= Sporoschisma (2)

Melogramma Fr.
= [?] Naemospora (1)

Phomatospora Sacc.
= Dinemasporium (1)
= Phoma (1)

Prosthecium Fres.
= Dothiorella (1)
= Hendersonia (1)
= Phomopsis vel aff. (3)
= Stilbospora (2)

Pseudovalsa Ces. & de Not.
= Coryneum (4)
= Fusicoccum (1)
= Phoma (1)

Pseudovalsella Höhn.
= Coryneum (1)

Sphaerognomonia Poteb.
= Monostichella (1)

Valsa Fr.
= Cytospora (32)
= Cytosporina (1)

Valsella Fckl.
= Cytospora (3)

Valseutypella Höhn.
= Cytospora (1)

Zignoella Sacc.
= Aposphaeria (2)

Diatrypaceae

Cryptosphaeria Grev.
= Cytosporina (2)

Diatrype Fr.
= Cytosporina (2)
= Libertella (2)
= Naemospora (1)
= Selenosporella (1)

Diatrypella (Ces. & de Not.) Sacc.
= Libertella (2)

Eutypa Tul.
= Cytosporina (5)

Eutypella (Nits.) Sacc.
= Cytospora (3)
= Cytosporina (3)
= Libertella (1)

Quaternaria Tul.
= Libertella (2)

Halosphaeriaceae

Ceriosporopsis Lind.
= chlamydospores (2)

Chadefaudia G. Feldm.
= unnamed coelomycete (pycnidial) (1)

Corollospora Werderm.
= Clavariopsis (1)

Halosphaeria Lind.
= [?] Periconia (1)
= Trichocladium (1)

Spathulospora Cav. & Johns.
= phialidic perithecial hairs (1)

Melanosporaceae

Ascotricha Berk.
= Dicyma (11)

Chaetomium Kunze ex Fr.
= Botryotrichum (1)
= Humicola (1)
= Papulaspora (1)
= Scopulariopsis (1)
= Trichocladium (1)

Farrowia D. Hawksw.
= Botryotrichum (3)

Lophotrichus Benj.
= Humicola (1)

Melanospora Corda
= Acremonium (1)
= [?] "Chlamydomyces" (1)
= Harzia (3)
= Paecilomyces vel aff. (1)
= Proteophiala (1)

Microthecium Corda
= [?] Acremonium (4)
= [?] Paecilomyces (4)

Polystigmataceae

Diachora J. Müller
= Diachorella (1)

Glomerella Spauld. & Schrenck
= Colletotrichum (16)

Ophiodothella (P. Henn.) Höhn.
= unnamed coelomycete (1)

Phyllachora Nits. apud Fuckel
= Leptostroma (1)
= Leptostromella (1)
= Phloeospora (1)
= Phyllosticta (1)
= Placosphaerella (1)
= Phyllosticta (1)
= Placosphaeria (1)

Plectosphaera Theiss.
= unnamed coelomycete (pycnidial) (1)

Polystigma DC. ex Chev.
= Polystigmina (1)

Sordariaceae

Apodospora Mirza & Cain
= unnamed phialidic hyphomycete (2)

Apiosordaria Arx & Gams
= Cladorrhinum (1)

Arnium Nits. apud Fuckel
= Haplosporium (1)

Bombardia Fr.
= Phialophora vel aff. (1)

Coniochaeta (Sacc.) Massee
= Phialophora (5)

Diplogelasinospora Cain
= chlamydospores (2)

Helminthosphaeria Fuckel
= Diplococcium (1)

Lasiosphaeria Ces. & de Not.
= Phialophora (1)

Neurospora Shear & Dodge
= Monilia (3)

Podospora Ces.
= Phialophora vel aff. (12)

Triangularia Boedijn
= Phialophora (3)

Tripterospora Cain
= [?] Acremonium (1)
= [?] Phialophora (1)

Zopfiella Winter
= [?] Acremonium (1)
= Chrysosporium (1)
= Humicola (1)
= [?] Phialophora (1)
= aleuriospores (1)

Sphaeriaceae

Acanthotheciella Höhn.
= Ypsilonia (3)

Anthostoma Nits.
= Cytospora (1)
(= Naemospora sp.)

Chaetosphaerella Müller & Booth
= Oedemium (2)

Chaetosphaeria Tul.
= Catenularia (4)
= Chloridium (4)
= Cladotrichum (2)
= Codinaea (4)
= Menispora (1)
= Phialocephala (1)
= Stachybotrys (1)
= Zanclospora (1)

Eriosphaeria Sacc.
= Sporidesmium (1)

Melanopsamma Niessl
= Stachybotrys (1)
Melanopsammella Höhn.
= Gonytrichum (1)
Nematostoma Syd.
= Chaetosticta (2)
[?] Nematothecium Syd.
= Atractilina (1)
Plectosphaerella Kleb.
= Fusarium (1)
Niesslia Auersw.
= Monocillium (4)
Pleocryptospora J. Reid & Booth
= ascospores bud in the ascus (1)
Thyridaria Fuckel
= Diplodia (1)
Trichosphaerella Bomm., Rouss. & Sacc.
= Acremonium (1)

Valsaceae
Peroneutypella Berl.
= Phaeoisaria (1)

Verrucariaceae
Pharcidia Korber
= unnamed coelomycetes (2)

Xylariaceae
Anthostomella Sacc.
= Cryptocline (1)
Daldinia Ces. & de Not.
= Nodulisporium (1)
= [?] Virgariella (1)
Graphostoma Piroz.
= Nodulisporium (1)
Hypoxylon Bull. ex Fr.
= Acrostaphylus (3)
= Nodulisporium (14)
= Triplicaria (1)
= Virgariella (6)
= Xylocladium (3)
Nummularia Tul.
= Xylocladium (1)
Nummulariola House
= Nodulisporium (1)
= Xylocladium (1)
Penzigia Sacc. & Paol. emend. Petch
= unnamed sporodochial hyphomycete (1)
Poronia Willd.
= Nodulisporium (1)
= Xylocladium (2)
Rosellinia de Not.
= Nodulisporium (4)
= [?] Stachylidium (1)
Xylosphaera Gray
= Nodulisporium (1)
= Padixonia (1)
[?] Discoxylaria Lindquist & Wright
= Hypocreodendron (1)
[?] Khuskia Hudson
= Nigrospora (1)
[?] Myrmaeciella Lindau
= Patellina (1)
[?] Phanerococcus Theiss. & Syd. (? = Koordersiella Höhn.)
= Phanerococculus (1)
[?] Remispora
= Periconia (1)

[?] Subbaromyces Hesseltine

= unnamed hyphomycete: (conidiogenesis similar to that in Scopulariopsis) cf. Bainieria

[?] Wallrothiella Sacc.

= Acremonium (1)
= Gliomastix (1)

Taphrinales

Taphrinaceae

Taphrina Fr.

= Rhodotorula (1)

Tuberales

Tuberaceae

Stephensia Tul.

= holoblastic hyphomycete (1)

REPORT OF THE UNITUNICATE COMMITTEE

Prepared by Dr. J. Webster for the Committee:
Drs. Hennebert, Malloch, Nag Raj, Subramanian and Webster

The recommendations of the Committee can be enumerated as follows:

(1) more attention should be paid to methods of stimulating ascospores to germinate. Mycologists often admit defeat in this area, yet a better understanding of the physiology of ascospores of many more species to germinate, we could make many more teleomorph-anamorph connections, since this is in most cases the simplest route from one to the other. It is often much more complicated and difficult to persuade anamorphic cultures to develop the teleomorph: this may entail making multiple matings, with no certainty of success. The factors involved in ascospore germination include chemical stimulation, time and temperature, among others. These remain to be investigated in many species.

(2) a second area in which basic research is still needed is that of the conditions which will induce fruiting in pure culture. As Dr. Müller has shown in Chapter 16, these may be highly specific, and may be entirely different even for different species within a single genus.

(3) We were reluctant to pinpoint specific fungal groups as requiring attention, since our ignorance is still so great in most; but we did consider that the genus *Mollisia* is in need of revision, since it seems to be little more than a discomycete dumping ground.

(4) We also felt that mycologists often tend to study teleomorphs or anamorphs in isolation, and we would like to recommend that a serious attempt should always be made to consider all known morphs whenever new taxa are to be described, or existing ones revised. This recommendation implies that where an unnamed anamorph is found connected with its teleomorph, it should be fully described and not simply designated, as for example, *Acremonium*-like or *Phialophora*-like. We note, however, that it will not always be possible to ascribe an appropriate generic name to the anamorph. Two-way communication between anamorph and teleomorph specialists is very desirable at such junctures.

(5) We strongly recommend also that whenever a new taxon is described, appropriate illustrations be provided of all morphs available. In many cases a judicious combination of photomicrographs and camera lucida line drawings is highly desirable. Line drawing are interpretations, and as such can reflect inaccurate or misleading conclusions (they may also reflect inadequate drawing technique!). Photomicrographs are not open to these criticisms, but they have very limited depth of focus, and to take good ones often requires prolonged searching of meticulously prepared slides. When both micrographs and drawings are provided, the author is making the strongest possible case for his new taxon, and the reader can assimilate and recognize it more easily. The better illustrated a new taxon is, the less chance there is of subsequent conceptual confusion.

A subcommittee of the Nomenclature Committee has recently been considering the matter of the registration of new names, etc. They discussed a possible requirement for illustration of all new taxa, but did not act on it. This Conference regrets that lost opportunity and recommends that a requirement for illustration of new taxa be embodied in the Code at the earliest opportunity. We acknowledge that excellence cannot be legislated, but we consider

that even a poor picture is better than none. Several members of the Conference expressed the view that pictures are more important than a Latin diagnosis, because they represent a far more universal language. It was also noted that the necessity of producing a drawing forces the author to make more critical observations than might be the case if no such requirement existed.

Article 38 of the Code now states that "In order to be validly published, a name of a new taxon of fossil plants of specific and lower rank published on or after 1st January 1912 must be accompanied by an illustration or figure." The recommendation supported by this Conference is essentially a modification of that Article, more or less as follows:

"In order to be validly published, a name of a new taxon of fossil plants and all fungi, fossil and recent, of specific or lower rank, must be accompanied by an illustration or figure, showing the distinctive morphological features, in addition to a Latin description or diagnosis, or by reference to a previously and effectively published illustration or figure. Fungus taxa based on biochemical distinctions are excluded from this ruling." In its essentials, this proposal will be formally presented to the Nomenclature Committee and promulgated through the proper channels, as being supported by a large majority of this Conference. A similar requirement for illustration of new taxa of recent algae has been in force since 1958.

(6) Particular attention should be paid in coelomycetous anamorphs to the ontogeny both of the conidioma itself and of the conidia it contains. This information is conspicuously absent in all but the most recent work on these anamorphs.

DIALOGUE FOLLOWING THE REPORT OF THE UNITUNICATE COMMITTEE

DE HOOG: I support the recommendations in themselves, but not as official ones from this Conference.

PIROZYNSKI: We have to make a definite nomenclatural proposal if we want a change in the Code.

MULLER: I think we represent part of the mycological public, and we also have a parliament -- the Nomenclatural Committee -- and we can help them by expressing our opinion as a group. We cannot decide the issue, we can only make a recommendation.

WERESUB: Proposals for change in the Code can be made by anyone. But either you publish it as a proposal for consideration at the next Botanical Congress, and do so formally, or it will be lost. You might send it to the Secretary of the I.A.P.T. Nomenclatural Committee, Ron Petersen. He is also Editor of the Nomenclatural section of Taxon.

MADELIN: If the book arising from this Conference plays as important a role in teaching as that which came out of Kananaskis-I, I think the opinion or recommendation, or whatever we call it, is likely to colour the views of the next generation of graduates; it will have an effect, whether it is officially promulgated or not.

CARMICHAEL: I think mycologists should not be free to propose new names at will. We should impose as many restrictions as we can to ensure that the names are properly attached to some kind of fungus, because the names are immortal, whether attached to anything or not. Once they are validly published they cannot be destroyed.

KENDRICK: Nor can they be salvaged and used again. We already carry an enormous millstone of absolutely non-functional but equally indestructible names around our collective neck. I would welcome any reasonable measures that would prevent the burden from becoming heavier each year. We are now living with the results of many years of virtual anarchy.

CARMICHAEL: Yes, so I don't go along with the argument that we shouldn't restrict people. I think they should be made to do a proper job.

KENDRICK: Hear hear! Dr. Carmichael and I live daily with the millstone as we compile the generic names and concepts in the Hyphomycetes. Our earlier comment on the problem appeared on page 329 of 'The Fungi' volume 4A (Kendrick and Carmichael 1973). Anything that makes the lives of future compilers easier would, I'm sure, bring down blessings on our heads.

WERESUB: If you look back at much of the earlier literature you will find that many authors did not give illustrations. If we had been deprived of their work by the existence of a rule requiring illustrations, a great deal of the knowledge on which we base conclusions today would be missing.

KENDRICK: Why would it have hurt them to make drawings of their new taxa? I happen to know that Spegazzini, though he never illustrated his papers, made beautiful, detailed and accurate sketches on his herbarium packets. We would have appreciated this artistry in his publications.

WERESUB: Some people just cannot draw -- you are looking at one.

BENJAMIN: I believe that almost anybody can learn to make acceptable camera-lucida drawings of fungi. I had a student who, when he began, couldn't draw for sour apples, yet he became a pretty good illustrator by the time he was through.

EDITOR: At this point several people spoke at once, the majority supporting Dr. Benjamin's position. It was also pointed out that photomicrographs are now an accessible alternative for the artistically inept. By a vote of 17 for, with two abstentions, the Conference approved the promulgation of the recommendations arrived at in discussion.

TELEOMORPH-ANAMORPH CONNECTIONS

ALPHABETICALLY BY BITUNICATE ASCOMYCETE GENUS

1.1.	Acanthostigmella thaxteri Linder (unitunicate fide Pirozynski pers. comm.)	
	= Xenosporium thaxteri (Linder) Piroz.	Pirozynski (1966)
2.2.4.	Achaetobotrys affine (Fraser) Bat. & Cif.	
	= Antennariella sp.	Hughes (1976)
2.2.4.	Acrogenotheca elegans (Fraser) Cif. and Bat.	
	= unnamed coelomycete (pycnidial)	Hughes (1967,1976)
	Agostaea niger (Viégas) Thirum. & Jenkins	
	= Tubercularia nigra Stevens	Stevens (1930)
2.2.4.	Aithaloderma capensis Doidge	
	= unnamed pycnidial coelomycete	Hughes (1976)
2.2.4.	A. citri ('Arnaud') Woron.	
	= Ciferrioxyphium sp.	Hughes (1976)
2.2.4.	A. clavatisporum H. & P. Sydow	
	= unnamed coelomycete (pycnidial)	Hughes (1976)
2.2.4.	A. ferruginea Fraser	
	= unnamed pycnidial coelomycete	Hughes (1976)
2.2.4.	A. viridis Fraser	
	= [?] Microxiphium viride Bat. & Cif.	Batista & Ciferri (1963), Hughes (1976)
2.2.4.	Aithaloderma sp.	
	= Ciferrioxyphium chaetomorphum (Speg.) Hughes	Hughes (1976)
	Alina jasmini Rac.	
	= Septoidium sp.	
	= Sporidesmium jasminicola M.B. Ellis	Ellis (1971), Arx & Müller (1975)
	Allosoma cestri Syd.	
	= Periconiella cestri (Syd.) M.B. Ellis	Ellis (1971)
2.2.4.	Antennulariella sp.	
	= 'Antennariella unedonis (Maire & Sacc.) Bat. & Cif. pro parte'	
	= Capnodendron trichomericola (Cif., Bat. & Nasc.) Hughes	
	= Microxiphium unedonis Bat. & Cif.	Hughes (1976)
2.2.4.	Apiosporina collinsii (Schw.) Höhn.	
	= Fusicladium vel aff.	Höhnel (1910), Barr (1968), Arx & Müller (1975), Wehmeyer (1975)
	= unnamed pycnidial coelomycete	
2.2.4.	A. morbosa (Schw. ex Fr.) Arx	
	= Cladosporium sp.	Barr (1968), Arx & Müller (1975)
2.2.2.	Arthonia culmicola Petr.	
	= Septocyta sp.	Jung (1957)
1.1.	Ascomycetella quercina Peck	
	= Articularia quercina (Peck) Höhn.	Peck (1881), Charles (1935)
	Asterina clasterosporium Hughes	
	= Clasterosporium sp.	Ellis (1958)
2.2.2.	A. diplocarpa Cooke	
	= Asterostomella diplocarpa Farr	Farr (1969)
2.2.2.	A. paraguayensis (Speg.) Speg.	
	= Asterostomella sp.	Farr (1969)
1.1.	Asterodothis solaris (Kalchbr. & Cooke) Theiss.	
	= Asterostromina sp.	
	= Clasterosporium vel aff.	Arx & Müller (1975)
1.1.	Atopospora betulina (Fr.) Petr.	
	= Didymochora betulina Höhn.	Arx & Müller (1975)
2.2.2.	Aulographina eucalypti (Cooke & Mass.) Arx & Müller	
	= Thyrinula eucalyptina Petr. & Syd.	Petrak & Sydow (1924)
2.3.1.	A. pinorum (Desm.) Arx & Müller	
	= Bahusakala sp.	Müller, Harr & Sulmont (1969)

1.1.	Bagnisiella examinans (Mont. & Berk.) Arx & Müller	
	= Haplosporella sp.	Arx & Müller (1975)
2.2.2.	Balladyna vanderystii (Hansf.) Arx	
	= Clasterosporium sp.	Ellis (1958,1976), Arx & Müller (1962)
	= Tretospora sp.	
2.2.2.	B. vanderystii (Hansf.) Arx var. ferulae-foetidae Thaung	
	= Clasterosporium sp.	Thaung (1976)
2.2.4.	Batistinula gallesiae Arx	
	= Triposporium vel aff.	Ainsworth et al. (1973), Arx & Müller (1975)
2.2.2.	Botryosphaeria berengeriana de Not.	
	= Dothiorella sp.	Arx & Müller (1975)
2.2.2.	B. dothidea (Moug. ex Fr.) Ces. & de Not.	
	= Dothiorella sp.	Arx & Müller (1954)
2.3.1.	B. fuliginosa (Moug. & Nestler) Ell. & Ev.	
	= [?] Sphaeropsis malorum Peck	Edgerton (1912), Stevens (1925)
2.3.1.	B. laricis (Wehm.) Arx & Müller	
	= Macrophoma sapinea (Fr.) Petr.	Smerlis (1970)
2.2.2.	B. melanops (Tul.) Wint. in Rabenh.	
	= Dothiorella advena Sacc.	
	= Macrophoma vel aff.	Shear & Davidson (1936), Shoemaker (1964)
2.2.2.	B. obtusa (Schw.) Shoem.	
	= [?] Sphaeriopsis malorum Peck	Shoemaker (1964)
2.2.2.	B. quercuum (Schw.) Sacc.	
	= Sphaeropsis sumachi (Schw.) Cke. & Ellis	Arx & Müller (1954)
	B. rhodina (Berk. & Curt.) Arx	
	= Lasiodiplodia (Botryodiplodia) theobromae (Pat.) Griff. & Maubl.	Arx & Müller (1975)
2.2.2.	B. ribis Grossenbacher & Duggar	
	= [?] Sphaeropsis vel aff.	Punithalingam & Holliday (1969)
].].].	B. stevensii Shoem.	
	= Diplodia mutila (Fr.) Mont.	Shoemaker (1964)
2.3.1.	B. subglobosa (Botoh apud Punithal.) Arx & Müller	
	= Sphaeropsis subglobosa Cooke	Punithalingam (1969), Arx & Müller (1975)
2.3.1.	B. tsugae Funk	
	= Macrophoma sp.	Funk (1964)
	B. visci (Kalchbr.) Arx & Müller	
	= Botryosphaerostroma visci (D.C.) Petr. & Syd.	Petrak & Sydow (1927)
2.2.2.	Brooksia tropicalis Hansf.	
	= Capnogoniella sp.	
	= Hiospira hendrickxii (Hansf.) R.T. Moore	Hughes (1976)
	Buergenerula sp.	
	= Rhynchosporina vel aff.	Carmichael et al. (1979)
2.2.4.	Capnodium anonae Pat.	
	= Scolecoxyphium spp.	Hughes (1976)
2.2.2.	C. salicinum Mont.	
	= Fumagospora capnodioides Arn.	Arx & Müller (1975), Hughes (1976)
2.2.4.	C. walteri Sacc.	
	= Phaeoxyphiella morototoni Bat. & Cif.	Hughes (1976)
1.1.	Caryospora sp.	
	= Asterostomella sp.	Arx & Müller (1975)
2.2.4.	Chaetothyrium concinnum Petr.	
	= Merismella concinna Petr.	Petrak (1925), Hughes (1976)
1.1.	Chevalieropsis ctenotricha (Pat. & Har.) Arnaud	
	= Septoidium vel aff.	Arx & Müller (1975)

2.2.4.	Clypeolella craterispermi Hansf. = Mitteriella vel aff.	Müller & Arx (1962)
2.2.4.	C. gymnospermae Hansf. = Mitteriella sp. = Sarcinella sp.	Hansford (1946)
2.2.4.	C. inversa Höhn. = Clasterosporium sp. = Mitteriella sp. = Sarcinella sp.	Arx & Müller (1975)
2.2.4.	C. psychotriae (Doidge) Doidge = Sarcinella sp.	Farr (1969), Pirozynski & Shoemaker (1970)
2.2.4.	C. rhamnicola (Doidge) Doidge = Sarcinella sp.	Farr (1969), Pirozynski & Shoemaker (1970)
2.2.4.	C. ricini Rac. apud Theiss. = Mitteriella sp. = Sarcinella sp.	Müller & Arx (1962)
2.3.1.	Clathrospora diplospora (Ell. & Ev.) Wehm. = Alternaria alternata (Fr.) Keissler	Simmons (1952)
2.3.1.	C. elynae Rab. = Alternaria alternata (Fr.) Keissler	Simmons (1952)
2.3.1.	Cochliobolus bicolor Paul & Parb. = Drechslera bicolor (Mitra) Subram. & Jain	Paul & Parbery (1966), Ellis (1971)
2.3.1.	C. carbonum Nel. = Drechslera sp.	Nelson (1959), Ellis (1971)
2.3.1.	C. cymbopogonis Hall & Siv. = Curvularia cymbopogonis (Dodge) Groves & Skolko	Hall & Sivanesan (1972)
2.3.1.	C. cynodontis Nel. = Drechslera cynodontis (Marig.) Subram. & Jain	Ellis (1971)
2.3.1.	C. geniculatus Nel. = Curvularia geniculata (Tracy & Earle) Boed.	Nelson (1964)
2.3.1.	C. heterostrophus (Dresch.) Dresch. = Bipolaris maydis (Nisi.) Shoem.	Drechsler (1934), Shoemaker (1959), Nelson (1960)
2.3.1.	C. intermedius Nel. = Curvularia intermedia Boed.	Nelson (1960)
2.3.1.	C. lunatus Nel. & Haas. = Curvularia lunata (Wakker) Boed.	Ellis & Gibson (1975)
2.3.1.	C. miyabeanus (Ito. & Kurib.) Drechs. ex Dastur = Bipolaris oryzae (B. de Haan) Shoem.	Shoemaker (1950), Nelson (1960)
2.3.1.	C. nodulosus Luttrell = Drechslera nodulosa (B. & C.) Subram. & Jain	Ellis (1971)
2.3.1.	C. sativus (Ito & Kurib.) Drechs. ex Dastur = Bipolaris sorokiniana (Sacc. in Sorok.) Shoem.	Shoemaker (1955,1959), Nelson (1960)
2.3.1.	C. setariae (Ito & Kurib.) Drechs. ex Dastur = Drechslera setariae (Sawada) Subram. & Jain	Nelson (1960), Ellis & Gibson (1975)
2.3.1.	C. spiciferus Nel. = Drechslera sp.	Nelson (1964), Ellis (1971)
2.3.1.	C. victoriae Nel. = Bipolaris victoriae (Meehan & Murphy) Shoem.	Shoemaker (1959), Nelson (1960)
	Comoclathris planispora (Ell.) J. Harr = Alternaria sp.	Arx & Müller (1975)
2.3.1.	Cucurbitaria ahmadi Mirza = Camarosporium sp.	Mirza (1968)

2.2.2.	C. amorphae (Wallr.) Fckl. = Camarosporium amorphae Sacc., Diplodia amorphae (Wallr.) Sacc.	Mirza (1968)
2.3.1.	C. berberidis (Pers. ex Fr.) Gray = Pyrenochaeta berberidis (Sacc.) Brum.	Müller & Baumeister (1957)
2.2.2.	C. caraganae Karst. = Camarosporium caraganae Karst. = Dichomera elaeagni Karst.	Mirza (1968)
1.1.	C. coluteae (Rabt.) Auersw. = Diplodia coluteae Schnalb.	Mirza (1968)
2.3.1.	C. coronillae (Fr.) de Thüm. = Camarosporium sp.	Mirza (1968)
2.3.1.	C. cytisi Mirza = Camarosporium sp.	Mirza (1968)
2.2.2.	C. dulcamarae (Kunze ex Schmidt) Fr. = Diplodia dulcamarae Fkl. = Hendersonia sp.	Mirza (1968)
2.3.1.	C. elongata (Fr.) Grev. = Camarosporium sp. ([?] Camarosporium robiniae Sacc.) 2.2.2. = Diplodia robiniae Bomm., Hendersonia robiniae West.	Mirza (1968)
2.3.1.	C. emeri Mirza = Diplodia sp.	Mirza (1968)
2.3.1.	C. ignavis de Not. = Camarosporium xylostei Sacc. = Leptophoma sp.	Müller (1963), Mirza (1968)
2.3.1.	C. laburni (Pers. ex Fr.) de Not. = Camarosporium sp., Coniothyrium sp. = Diplodia sp., Hendersonia sp., Phoma sp.	Müller & Baumeister (1957), Mirza (1968)
2.2.2.	C. negundinis Winter = Camarosporium negundinis Ell. & Ev.	Mirza (1968)
2.2.2.	C. ononidis Mass. = [?] Camarosporium sp. = [?] Pyrenochaeta sp.	Mirza (1968)
	C. piceae Borthwick = Camarosporium strobilinum Bomm., Rouss. & Sacc.	
2.2.2.	C. rhamni (Nees. ex Fr.) Fuckel = Camarosporium rhamni Alles., Diplodia frangulae Fckl., Microdiplodia rhamni Fckl.	Mirza (1968)
2.2.2.	C. ribis Niessl = Diplodia ribis Sacc.	Mirza (1968)
2.3.1.	C. spartii (Nees ex Fr.) Ces. & de Not. = [?] Camarosporium sp.	Müller & Baumeister (1957), Mirza (1968)
2.3.1.	C. staphula Dearn. ex Arnold & Russ. = Pseudodichomera sp., [?] Macrophoma tumefaciens Shear	Arnold & Russell (1960)
2.2.2.	C. varians Hazsl. = Camarosporium sp., Diplodia sp.	Mirza (1968)
	Cucurbitaria sp. = Camarosporium (incl. Dichomera sp.) Diplodia sp., Phoma sp., (Pyrenochaeta sp.)	Arx & Müller (1975)
1.1.	Curreya pityophila (Fr.) Arx & Müller = Coniothyrium pityophilum (Höhn.) Petr. & Syd.	Arx & Müller (1975)
1.1.	Cyclopeltis sp. = Cyclopeltella sp.	Ainsworth et al. (1971)

2.2.2.	Delphinella abietis (Rostr.) Müller apud Müller & Arx	
	= Dothiorella sp. [Phoma bohemica Bubák & Kabat]	Barr (1972)
2.2.4.	Dennisiella babingtonii (Berk.) Bat. & Cif.	
	= Microxiphium fagi (Pers.) Hughes	Hughes (1976)
2.2.4.	Dennisiella spp.	
	= Microxiphium spp.	Hughes (1976)
1.1.	Dermatodothis sp.	
	= Hendersonia vel aff.	Müller & Arx (1975)
2.2.2.	Dibotryon sp.	
	= Cladosporium vel aff.	Sutton & Waterston (1970)
	Dictyotrichiella mansonii Schol-Schw.	
	= Rhinocladiella mansonii (Cast.) Schol-Schw.	Schol-Schwarz (1968), Ellis (1971)
2.3.1.	Didymella asphodeli Müller	
	= Phoma solieri (Mont.) Sacc.	
	= Phyllostictina solieri (Mont.) Petr. & Syd.	Müller (1958), van der Aa (1973)
	D. bryoniae (Auersw.) Rehm	
	= Ascochyta cucumis Fautr. & Roum.	Müller & Arx (1962)
	D. cannabis (Wint.) Arx apud Müller & Arx	
	= unnamed pycnidial coelomycete (?) Phoma sp.	Müller & Arx (1962)
2.2.2.	D. exigua (Niessl) Sacc.	
	= Ascochyta sp., Dendrophoma sp.	
	= Phoma sp., Plenodomus sp.	Müller & Arx (1962)
2.3.1.	D. festucae (Weg.) Holm.	
	= Phloeospora idahoensis Sprague	Smith & Shoemaker (1974)
2.2.1.	D. heribaudii Har. & Br.	
	= Phoma jacquiniana Cke. & Mass.	Grove (1935)
2.2.2.	D. hyphensis Sacc.	
	= Leptostromella pteridina Sacc. & Roum.	Grove (1937)
2.2.2.	D. lycopersici Kleb.	
	= Ascochyta lycopersici (Plowr.) Brun.	Grove (1937), Holliday & Punithalingam (1970)
	D. pinodes (Berk. & Blox.) Petr.	
	= Ascochyta pinodes Jones	Müller & Arx (1962)
2.3.1.	D. vodaki Müller	
	= Ascochyta vodaki Bub.	Müller (1953)
	D. winteriana (Sacc.) Petr. apud Munk	
	= Phoma vel aff.	Müller & Arx (1962)
	Didymellina ornithogali E. Jacques	
	= Heterosporium ornithogali (Kl.) Cke.	Shaw (1973)
	D. paecilospora McWhorter	
	= Heterosporium cladosporioides McWhort.	McWhorter (1937)
2.3.1.	Didymosphaeria brunneola Niessl	
	= Dendrophoma sp.	Müller & Corbaz (1956)
	D. futilis (B. & Br.) Rehm	
	= Dendrophoma (Phoma) sp., Fusicladiella vel aff.	Arx & Müller (1975)
2.3.1.	D. igniaria Booth	
	= Periconia igniaria Mason & M.B. Ellis	Booth (1968)
2.3.1.	D. spartii (Cast.) Fabre	
	= Dendrophoma sp.	Müller & Corbaz (1956)
1.1.	Dimerina andirae (P. Henn.) Hansf.	
	= Ectosticta sp.	Arx & Müller (1975)
1.1.	Dimerium pulveraceum (Speg.) Theiss.	
	= Cicinnobella sp., Ectosticta sp.	Arx & Müller (1975)
2.2.2.	Dimerosporium tropicale Speg. (= Asterina Lév. fide Arx & Müller (1975))	
	= Cicinnobella tropicale (Speg.) Farr	Farr (1969)
2.3.1.	Dothidea acerva Barr	
	= Aureobasidium pullulans (Laff.) Herm.-Nijh. vel aff.	Loeffler (1957), Barr (1972)

1.1.	D. barringtoniae B. & Br.	
	= Phoma barringtoniae Cke. & Mass.	Grove (1937)
	Dothidea sp.	
	= Asteromellopsis sp., [?] spermatial	
	= Systremmopsis sp., [?] spermatial	Loeffler (1957)
2.3.1.	Dothiora polyspora Shear & Davids.	
	= Dothichiza sp.	Shear & Davidson (1940)
2.3.1.	D. pyrenophora (Fr.) Fr.	
	= Dothichiza sorbi Lib.	Shear & Davidson (1940), Barr (1972)
2.2.2.	D. sphaeroides (Pers. ex Fr.) Fr.	
	= Dothichiza tremulae (Sacc.) Höhn.	Barr (1972)
2.3.1.	D. taxicola (Petr.) Barr	
	= Cytospora taxifolia Cke. & Mass.	
	= Dothichiza sp.	Barr (1972)
	Dothiora sp.	
	= Aureobasidium sp.	
	= Dothichiza sp.	
	= Hormonema sp.	Arx & Müller (1975), Hermanides-Nijhof (1977)
2.2.2.	Discosphaerina discophora Höhn.	
	= [?] Cercosporella sp.	Petrak (1921), Hudson (1966)
2.3.1.	Elsinoë ampelina (de Bary) Shear	
	= Sphaceloma ampelinum de Bary	Shear (1929), Bitancourt & Jenkins (1943)
2.2.2.	E. australis Bitanc. & Jenk.	
	= Sphaceloma australis Bitanc. & Jenk.	Bitancourt & Jenkins (1936)
2.2.2.	E. canavaliae Racib.	
	= Sphaceloma sp.	Sivanesan & Holliday (1971)
2.3.1.	E. cinnamomi Pollack & Jenk.	
	= Sphaceloma sp.	
	= unnamed pycnidial coelomycete	Limber, Pollack & Jenkins (1946)
2.2.2.	E. fawcettii Bitanc. & Jenkins	
	= Sphaceloma fawcettii Jenk.	Bitancourt & Jenkins (1936)
2.3.1.	E. euonymi-japonici Jenk. & Bitanc.	
	= Sphaceloma euonymi-japonici Kuro. & Kats.	Jenkins & Bitancourt (1957)
	E. heveae Bitanc. & Jenk.	
	= Sphaceloma heveae Bitanc. & Jenk.	
2.2.2.	E. phaseoli Jenk.	
	= Sphaceloma sp.	Sivanesan & Holliday (1971)
2.2.2.	E. piri (Woron.) Jenk.	
	= Sphaceloma pirinum (Pegl.) Jenk.	Shaw (1973)
2.2.2.	E. quercus-falcatae Miller	
	= Sphaceloma sp.	Miller (1957)
	E. quercus-ilicus (Arn.) Jenk. & Goid.	
	= Sphaceloma quercus-ilicus Mart. & Lav.	
2.2.2.	E. rhynchosiae Jenk. & Watson	
	= Sphaceloma sp.	Jenkins & Watson (1962)
2.2.2.	E. rosarum Jenk. & Bitanc.	
	= Sphaceloma rosarum (Pass.) Jenk.	Jenkins & Bitancourt (1957)
2.3.1.	E. sesbaniae Limber & Jenkins	
	= Sphaceloma sp.	Limber, Pollack & Jenkins (1946)
2.2.2.	E. spondiadis Watson & Jenk.	
	= Sphaceloma spondiadis Bitanc. & Jenk.	Watson & Jenkins (1969)
2.2.2.	E. veneta (Burk.) Jenk.	
	= Sphaceloma necator (Ell. & Ev.) Jenk. & Shear	Shaw (1973)
2.2.2.	Elsinoë sp.	
	= Sphaceloma sp.	Jenkins & Bitancourt (1941)
2.2.4.	Euantennaria caulicola Hughes	
	= Antennatula caulicola (Bat. & Oliveira) Hughes	
	= Hormisciomyces sp.	Hughes (1974)

2.2.4.	E. mucronata (Mont.) Hughes	
	= Antennatula sp.	
	= Hormisciomyces sp.	Hughes (1974)
2.2.4.	E. novae-zealandica Hughes	
	= Antennatula sp.	
	= Hormisciomyces sp.	Hughes (1974)
2.2.4.	E. pacifica Hughes	
	= Antennatula sp.	
	= Hormisciomyces sp.	Hughes (1974)
2.2.2.	Eudarluca australis (Fr.) O. Eriksson	
	= Darluca filum (Fr.) Cast.	Müller & Arx (1962), Eriksson (1966)
2.2.2.	E. caricis (Fr.) O. Erikss.	
	= Darluca sp.	
	= Metabotryon sp.	Eriksson (1966)
2.2.2.	E. connata (Syd.) Arx apud Müller & Arx	
	= Metabotryon connata Syd.	Sydow (1926), Müller & Arx (1962)
	Eutryblidiella hysterina (Dufour) Petr.	
	= Diplodia vel aff.	
	= Phoma vel aff.	Arx & Müller (1975)
2.2.2.	Eupelte rapaneae Hansf.	
	= Sporidesmium sp.	Ellis (1958)
2.2.2.	E. farrae (Piroz. & Shoem.) Arx & Müller	
	= Clasterosporium vel aff.	
	= Septoidium vel aff.	Arx & Müller (1975)
2.2.2.	Farlowiella australis Dennis	
	= Acrogenospora sp.	Ellis (1972)
2.2.2.	F. carmichaeliana (Berk.) Sacc.	
	= Acrogenospora sphaerocephala (B. & Br.) M.B. Ellis	Bisby & Hughes (1952), Ellis (1971)
	Gemmamyces piceae (Borth.) Casag.	
	= Megaloseptoria mirabilis Naumov	Casagrande (1969)
2.2.2.	Gibbera distegiae (Tracy & Earle) Barr	
	= unnamed hyphomycete	Barr (1968)
2.2.2.	G. vaccinicola (Dearn. & House) Barr	
	= unnamed hyphomycete	Barr (1968)
1.1.	G. vaccinii (Sow. ex Fr.) Fr.	
	= Helminthosporium vaccinii Fr.	Shear (1948), Barr (1968)
1.1.	G. vitis Sch.	
	= Phoma vitis Bon.	Grove (1937)
2.3.1.	Gibberidea visci Fckl.	
	= Pleurostromella visci Petr.	Müller (1953), Holm (1968), Arx & Müller (1975)
2.2.2.	Gilletiella chusqueae (Pat.) Sacc. & Syd.	
	= Ascochyta vel aff.	Farr (1966) Arx & Müller (1975)
1.1.	Gillotia opuntiarum (Speg.) Arx & Müller	
	= Asteromella vel aff.	Arx & Müller (1975)
2.2.4.	Glyphium leptothecium (Earle) Sutton	
	= Peyronelia sp.	Sutton (1970)
2.2.4.	G. schizosporum (Maire) Zogg	
	= Peyronelia sp.	Sutton (1970)
2.3.1.	Guignardia aesculi (Pk.) Stew.	
	= Asteromella sp.	
	= Phyllostictina sphaeropsoidea Ell. & Ev.	van der Aa (1973), Müller (1957)
2.3.1.	G. aleuritidis (Vassil.) van der Aa	
	= Phyllostictina africana Pand. & Hus.	van der Aa (1973)
	G. ardisiae (Miura) Hiro & Katum.	
	= Phyllosticta sp.	Kobayashi (1973)
2.3.1.	G. bidwellii (Ell.) Vial. & Ravaz	
	= Asteromella sp.	
	= Phyllostictina sp.	Müller (1957)

2.2.2.	G. boltoniae Dearn. & Barth. apud Dearn. = Asteromella sp. = Macrophoma boltoniae Dearn. & Barth. = Phoma boltoniae Dearn. & Barth. = Selenophoma sp.	Dearness (1926), Müller (1957)
2.3.1.	G. bulgarica (Petr.) Müller = Selenophoma sp.	Müller (1957)
2.3.1.	G. calami (Syd.) Arx & Müller = Phyllosticta arecae Höhn.	van der Aa (1973)
2.2.2.	G. carpogena (Atk.) Shear = Phyllostictina sp.	Müller (1957)
2.3.1.	G. citricarpa Kiely = Phyllostictina citricarpa (McAlp.) van der Aa	van der Aa (1973)
2.3.1.	G. concinna (Syd.) van der Aa = Phyllosticta concinna (Syd.) van der Aa	van der Aa (1973)
2.3.1.	G. crepidis Müller = Selenophoma sp.	Müller (1957)
2.3.1.	G. cytisi (Fckl.) Arx & Müller = Dothiorella spartiicola Petr. & Syd. = Selenophomopsis juncea Mont. & Petr.	Arx & Müller (1954), Müller (1957)
2.3.1.	G. dioscoreae Pande = Phyllosticta dioscoreae Cooke	van der Aa (1973)
2.2.2.	G. epilobii (Wallr.) Lindau = Selenophoma epilobii Petr.	Klebahn (1918), Müller (1957)
2.3.1.	G. fagi Hudson = Aureobasidium vel aff.	De Hoog & Hermanides-Nijhof (1977)
2.2.2.	G. foeniculata (Mont.) Arx & Müller apud Müller = Selenophoma bupleuri Petr.	Müller (1957)
2.2.2.	G. franconica (Petr.) Müller = Selenophoma sp.	Müller (1957)
2.3.1.	G. fulvida Sanderson = Aureobasidium pullulans (Laff.) Herm.-Nijh.	De Hoog & Hermanides-Nijhof (1977)
2.3.1.	G. gaultheriae van der Aa = Phyllosticta gaultheriae van der Aa	van der Aa (1973)
2.2.2.	G. gentianicola (DC.) Arx & Müller = Selenophoma sp.	Müller (1957)
2.2.2.	G. himalayensis Müller = Kabatia sp.	Müller (1959)
2.2.2.	G. latemarensis Müller = Kabatia lonicerae (Harkn.) Höhn.	Müller (1953,1959)
2.2.2.	G. minuta Arx & Müller = Colletotrichella periclymeni Höhn.	Müller (1959)
2.2.2.	G. mirabilis Müller = Kabatia mirabilis Bub.	Müller (1959)
2.3.1.	G. miribelii van der Aa = Hormonema sp. = Sarcophoma miribelii (Fr.) Höhn.	van der Aa (1973), De Hoog & Hermanides-Nijhof (1977)
2.3.1.	G. morindae (Koorders) van der Aa = Phyllosticta morindae (Kooders) van der Aa	van der Aa (1973)
2.3.1.	G. musae Racib. = Phyllosticta musarum (Cooke) van der Aa	van der Aa (1973)
2.3.1.	G. niesslii (Knze.) Lindau = [?] Phyllosticta sp.	Müller (1957)
2.3.1.	G. philoprina (Berk. & Curt.) van der Aa = Phyllosticta concentrica Sacc.	van der Aa (1973)
2.2.2.	G. populi Thomp. = Septogloeum rhopaloideum Dearn. & Bisby	Thompson (1954)

2.2.2.	G. poterii (Petr.) Müller = Selenophoma sp.	Müller (1957)
2.3.1.	G. reticulata (DC. ex Fr.) van der Aa = Phyllosticta cruenta (Kunze ex Fr.) Kickx.	van der Aa (1973)
2.3.1.	G. rhodorae (Cke.) Davis = Asteromella saccardoi (Thüm.) Petr. = Phyllostictina maxima (Ell. & Ev.) Petr.	Davis (1946), Barr (1972)
2.2.2.	G. serratulae (Petr.) Müller = [?] Phyllostictina sp.	Müller (1957)
2.3.1.	G. stromatica (Fkl.) Petr. = Asteromella sp. = Phyllostictina sp.	Müller (1957)
2.3.1.	G. vaccinii Shear = Phyllosticta vaccinii Earle = Phyllostictina vaccinii Shear	Shear (1923), Barr (1972), van der Aa (1973)
2.1.	Herpotrichia vermicularispora (Hino & Katumoto) Piroz. = [?] Corynespora faveolata (Pat.) Hughes	Ellis (1960), Pirozynski (1972)
1.1.	Herpotrichia sp. = Pyrenochaeta sp.	Arx & Müller (1975)
2.3.1.	Hysterium insidens Schw. = Coniosporium sp. = Sirodesmium gramulosum de Not.	Lohman (1933), Tubaki (1958), Ellis (1971)
2.2.2.	H. karstenii Lohman = Coniosporium sp. sub Sporidesmium	Lohman (1939)
1.1.	Hysterium sp. = Coniosporium sp. = Hysteropycnis sp.	Arx & Müller (1975)
1.1.	Hysterographium sp. = Hysteropycnis sp.	Arx & Müller (1975)
2.2.4.	Hysterostomella tetracerae (Rud.) Höhn. = Poropeltis davilliae P. Henn.	Höhnel (1909)
2.2.1.	Karstenula ligustrina Petr. = Microdiplodia mamma Allesch.	Petrak (1919)
2.2.1.	K. rhodostoma (Alb. & Schw.) Sacc. = Microdiplodia frangulae Allesch.	Petrak (1919)
2.3.1.	Keissleriella sp. = Ascochyta sp. = Dendrophoma sp.	Bose (1961)
2.2.2.	Kiehlia bambusina (Speg.) Farr var. bambusina Farr = Placonema bambusacearum (Sacc. & Syd.) Petr. var. bambusae (Bat.) Sutt.	Ciccarone (1965), Barr (1968), Sutton (1976)
2.2.2.	K. bambusina (Speg.) Farr var. bambusarum (Shanor) Farr = Placonema bambusacearum (Sacc. & Syd.) Petr. var. bambusacearum Sutt.	Ciccarone (1965), Barr (1968), Sutton (1976)
2.3.1.	Lasiobotrys affinis Hark. = Ulocladium vel aff.	Bonar (1928)
2.2.2.	Laterotheca stevensonii Bat. apud Bat. & Cif. = unnamed pycnidial coelomycete = unnamed synnematous hyphomycete (...possibly based on discordant elements, Luttrell (1973))	Hughes (1976)
2.2.2.	Leptoguignardia onobrychidis Müller = Diplodina sp. = [?] Dothichiza vel aff.	Müller (1958), Arx & Müller (1975)
2.2.2.	Leptopeltopsis lunariae (Fckl.) Arx = Leptothyrium lunariae Kunze	Arx & Müller (1975)
2.3.1.	Leptosphaeria acuta (Fr.) Karst. = Phoma acuta Fckl.	Grove (1937), Müller & Tomašević (1957), Müller (1973)

2.3.1.	L. agnita (Desm.) Ces. & de Not.	
	= Phoma sp.	Lucas & Webster (1967)
2.3.1.	L. anemones Hollos	
	= Rhabdospora anemones Hollos	Müller (1950,1971)
2.3.1.	L. artemisiae (Fckl.) Auersw.	
	= Asteromella artemisiae Müller	Müller (1950), Lucas & Webster (1967)
1.1.	L. arundinacea Sacc.	
	= Stagonospora vexata Sacc.	Grove (1935), Lucas (1968)
1.1.	L. avenaria Web.	
	= Septoria avenae Frank	Grove (1935)
	L. bondari	
	= Coniothyrium sp.	Wehmeyer (1975)
2.3.1.	L. cistina Urries	
	= Hendersonia cisti Camara	Lucas (1968)
2.3.1.	L. conferta Niessl ex Sacc.	
	= Phoma sp.	Lucas (1963)
2.3.1.	L. congesta Lucas	
	= Phoma sp.	Lucas (1963)
	L. coniothyrium (Fkl.) Sacc.	
	= Coniothyrium fuckelii Sacc.	Zeller (1927), Moore (1959)
2.1	L. cruenta Sacc.	
	= Phoma sanguinolenta Rost.	Grove (1935)
	L. culmifraga (Fr.) Ces. & de Not.	
	= Phaeoseptoria sp.	Wehmeyer (1975)
2.3.1.	L. doliolum (Fr.) de Not.	
	= Phoma sp.	
	(= [?] Plenodomus sp.)	Lucas & Webster (1967)
2.3.1.	L. dumetorum Niessl	
	= Hendersonia sp.	
	= Phoma sp.	Lucas & Webster (1967)
2.3.1.	L. elaeidis Booth & Robertson	
	= Pestalotiopsis sp.	Booth & Robertson (1961), Barr (1975)
	Asci of L. elaedis are not bitunicate fide Müller (pers. comm.); the taxon may be a species of Pestalosphaeria Barr fide DiCosmo.	
2.3.1.	L. eustomoides Sacc.	
	= Hendersonia sp.	Webster & Hudson (1957)
2.3.1.	L. fuckelii Niessl apud Voss	
	= Phaeoseptoria sp.	Webster & Hudson (1957)
2.1.	L. gigaspora Niessl	
	= Stagonospora gigaspora Sacc.	Grove (1935)
2.3.1.	L. haematites (Rob.) Niessl apud Rabenh.	
	= Phoma sp.	Lucas & Webster (1967)
2.3.1.	L. heterospora (de Not.) Sacc.	
S	= Alternaria sp.	Simmons (1952), Müller (1953)
2.3.1.	L. honiaraensis Mats. ([?] Pestalosphaeria sp. fide DiCosmo)	
	= Pestalotia sp.	Matsushima (1971), Barr (1975)
2.3.1.	L. lactuosa Niessl apud Sacc.	
	= Phaeoseptoria sp.	Webster & Hudson (1957)
2.3.1.	L. ladina Müller	
	[= Cladosporium ladinum Müller C. ladinum was a contaminant fide Müller, pers. comm.]	Müller (1950)
2.3.1.	L. libanotis (Fckl.) Niessl	
	= Hendersonia sp.	
	= Phoma sp.	Lucas & Webster (1967), Wehmeyer (1975)
	L. lindquistii Frezzi	
	= Phoma macdonaldii Boerema	

2.3.1.	L. macrospora (Fckl.) Thuem.	
	= Phaeoseptoria sp.	
	= Rhabdospora bernaridana Sacc.	Müller (1953), Lucas & Webster (1967)
2.3.1.	L. maculans (Desm.) Ces & de Not.	
	= Camarosporium affine Sacc., Bomm. & Rouss.	
	= Phoma lingam (Tode ex Fr.) Desm.	Müller & Tomasevic (1957), Müller (1971)
2.3.1.	L. marcyensis (Pk.) Sacc.	
	= Diplodina sp.	Lucas & Webster (1967)
2.1.	L. maydis Stout	
	= Septoria zeae Stout	Stout (1930)
2.3.1.	L. millefolii (Fckl.) Niessl	
	= Camarosporium sp.	
	= Leptophoma sp.	Müller & Tomasevic (1957), Müller (1971)
2.3.1.	L. nigrans [(Rob. apud Desm.)] Ces. & de Not.	
	= Phaeoseptoria sp.	Hughes (1949)
2.1.	L. obiones (Crouan & Crouan) Sacc.	
	= Ascochytula obiones Died.	
	= Coniothyrium obiones Died.	Grove (1935)
2.3.1.	L. obtusispora Speg.	
	= Microdiplodia henriquesii (Thüm.) Petrak & Sydow	Petrak & Sydow (1925), Lucas (1963)
2.3.1.	L. ogilviensis (B. & Br.) Ces. & de Not.	
	= Camarosporium sp.	
	= Phoma sp.	Müller & Tomasevic (1957), Müller (1971)
2.3.1.	L. orthosanthi Müller	
	= Camarosporium sp.	Müller & Dennis (1965)
1.1.	L. phlogis Bos.	
	= Septoria phlogis Sacc. & Speg.	Grove (1935)
2.3.1.	L. polygonati Müller & Tom.	
	= Hendersonia sp.	
	= Stagonospora sp.	Müller & Tomasevic (1957), Müller (1971,1973)
2.3.1.	L. pontiformis (Fckl.) Sacc.	
	= Hendersonia sp.	
	= Phoma sp.	Webster & Hudson (1957)
2.3.1.	L. pratensis Sacc. & Briard. in Roum.	
	= Ascochyta melitoti (Trel.) Davis,	
	= Stagonospora meliloti (Lasch.) Petr.	Lucas & Webster (1967)
	L. pontiformis (Fckl.) Sacc.	
	= Hendersonia sp.	
	= Phoma sp.	Wehmeyer (1975)
2.3.1.	L. purpurea Rehm	
	= Phoma sanguiolenta Gr.	Lucas & Webster (1967)
2.3.1.	L. sacchari Breda de Haan	
	= Phyllosticta sp.	Hudson (1960)
2.3.1.	L. solani Rom. apud Berl.	
	= Phoma sp.	Lucas & Webster (1967)
1.1.	L. sorbi Jacz.	
	= Septoria sorbi Lasch	Grove (1935)
2.3.1.	L. spartinae Ell. & Ev.	
	= [?] Coniothyrium sp.	Lucas & Webster (1967)
2.3.1.	L. submaculans Holm	
	= Phoma sp.	Lucas & Webster (1967)
2.3.1.	Leptosphaeria taiwanensis Yen & Chi	
	= Cercospora taiwanensis Matsum. & Yam.	Sivanesan (1976)
2.2.2.	L. thomasiana Sacc. & Roum.	
	= Phoma sp.	Zeller (1927)
2.3.1.	L. typhicola Karst.	
	= Phoma sp.	Lucas & Webster (1967)
2.3.1.	L. viridella (Pk.) Sacc.	
	= Hendersonia sp.	Lucas & Webster (1967)

	L. vitalbae Niessl = Hendersonia sp.	Wehmeyer (1975)
2.3.1.	[?] Leptosphaeria sp. (? = Pestalosphaeria sp. fide DiCosmo) = Pestalotia palmarum Cke.	Hansen et al. (1956), Guba (1961), Barr (1975)
	Leptosphaerulina americana Graham & Lutt. = Stemphylium vel aff.	Kobayashi (1970)
	L. japonica Kasai = blastospores (yeast-like)	Kobayashi (1970)
2.3.1.	Leptosphaerulina sp. (sub Pseudoplea briosiana Poll.) Höhn. = Stemphylium botryosum Wallr.	Nelson & Kernkamp (1953)
2.2.2.	Lidophia graminis (Sacc.) Walker & Sutton = Dilophospora alopecuri (Fr.) Fr.	Walker & Sutton (1974)
2.2.2.	Limacinia fernandeziana Neger apud Johow, nomen dubium fide Hughes = Capnocybe sp. = Capnophialophora sp.	Hughes (1966,1976)
2.2.2.	L. fraserae Hughes = Capnocybe fraserae Hughes = Capnophialophora fraserae Hughes	Hughes (1966)
2.2.2.	L. moniliformia (Fraser) Barr = Capnocybe sp. = Capnophialophora sp.	Hughes (1966)
2.2.2.	L. quinqueseptata (Barr) Hughes = Capnocybe sp. = Capnophialophora sp.	Hughes (1966)
	Limacinia sp. = Capnocybe spongiosa (Hoerl.) Hughes	Hughes (1966)
	Limacinula javanica (Zimm.) Höhn. = ascospores w. conidiogenous cells	Hughes (1976)
1.1.	Lophiostoma sp. = unnamed coelomycete (pycnidial)	Chesters & Bell (1970), Arx & Müller (1975)
	Lophium mytilinum (Pers.) Fr. = Papulaspora mytilina (Pers.) Lohman	Tubaki (1958)
2.3.1.	Magnaporthe salvinii (Cattaneo) Krause & Web. = Nakataea sigmoidea (Cav.) Hara	Tullis (1932,1933), Krause & Webster (1972)
2.2.2.	Massaria eburnea Sacc. = [?] Rhabdospora princeps Sacc.	Grove (1935)
2.2.1.	M. foedans Fr. = Hendersonia ulmi Otth.	Grove (1937), Shoemaker & LeClair (1975)
1.1.	M. hippophaes Jacz. = [?] Cytospora hippophaes Thüm.	Grove (1935)
1.1.	M. loricata Tul. = Neohendersonia kickxii (West.) Sutton & Pollack	Grove (1935), Sutton & Pollack (1974)
2.2.2.	M. macrospora Sacc. (? = M. loricata) = Asterosporium hoffmanni Knze. = Diplodia faginea Fr. = Scolecosporium fagi Knze.	Grove (1937)
1.1.	M. niessleana Rehm = Myxocyclus polycystis (B. & Br.) Sacc.	Grove (1937), Sutton (1975)
2.3.1.	M. platani Ces. = Hendersonia desmazieri Mont. (= Stilbospora quadriseptata Schw.)	Shear & Davidson (1936)
1.1.	M. populina (Fr.) Tul. = Stilbospora ovata Pers. ex Mérat	Grove (1937), Sutton (1975)
2.3.1.	Massarina aquatica Webster = Dactylella aquatica (Ing.) Ranzoni	Webster (1965)
	M. parasitica Bose & Müller = Stagonospora sp.	

	Massarina sp.	
	= Anguillospora longissima (de Wild.) Ingold	Willoughy & Archer (1973), Ingold (1975)
2.2.4.	Maurodothina farriae Piroz. & Shoem.	
	= Pirozynskia farriae Subram.	Pirozynski & Shoemaker (1970), Ellis (1976)
2.3.1.	Melanomma fuscidum Sacc.	
	= Aposphaeria vel aff. (Phoma fuscidula Sacc.)	Chesters (1938)
2.3.1.	M. pulvis-pyrius (Pers.) Fckl.	
	= Aposphaeria vel aff.	Chesters (1938)
2.3.1.	M. seminis (Cke. & Hark.) Sacc.	
	= Aposphaeria sp.	
	= Phoma sp.	Bonar (1928), Chesters (1938)
2.3.1.	M. subdispersum (Karst.) Berl. & Vogl.	
	= Pseudospiropes sp.	Hughes (1950), Ellis (1976)
1.1.	Melanoplaca sp.	
	= Placomelan sp.	Ainsworth et al. (1971)
	Meliolina sp.	
	= Catenularia vel aff.	de Hoog (1977)
2.2.2.	Melioliphila adianti (Rehm.) Piroz.	
	= Chionomyces meliolicola (Ciferri) Deighton & Piroz.	Pirozynski pers. comm.
2.2.2.	M. melioloides (Speg.) Piroz.	
	= Eriomycopsis bonplandii Speg.	Pirozynski (1977)
2.2.2.	M. piliferum (Pat. & Gaill.) Piroz.	
	= Chionomyces chorleyi (Hansf.) Deighton & Piroz.	Pirozynski pers. comm.
2.2.4.	Metacapnodium fraserae (Hughes) Hughes	
	= Capnocybe fraserae Hughes	Hughes (1966,1976)
	M. juniperi (Phil. & Plowr.) Speg.	
	= Capnobotrys sp.	
	= Capnophialophora sp.	
	= Capnosporium sp.	Hughes (1972), Arx & Müller (1975)
2.2.2.	Metasphaeria culmifida Sacc.	
	= Septoria oxyspora Penz. & Sacc.	Grove (1935), Arx & Müller (1975)
1.1.	M. hederae Sacc.	
	= Phoma leucostigma Sacc.	Grove (1935)
2.1.	M. ocellata Sacc.	
	= [?] Diploceras hypericinum Died.	Grove (1935)
2.1.	M. rubella Sacc.	
	= Phoma rubella Gr.	Grove (1935)
2.2.2.	Microcyclus tinctoria (Tul.) Arx apud Müller & Arx	
	= Ascochyta baccharidis Pat.	
	= Clypeodiplodina baccharidis Stev.	
	= Pazschkeella brasiliensis Syd.	Müller & Arx (1962)
2.2.2.	M. ulei (P. Henn.) Arx apud Müller & Arx	
	= Aposphaeria ulei P. Henn.	
	= Fusicladium macrosporum Kuyper	Müller & Arx (1962), Sutton & Waterston (1970)
	Microcyclus sp.	
	= Cercospora sp.	
	= Passalora sp.	de Hoog (1977)
2.3.1.	Muellerites juniperi (Müller & Arx) Holm	
	= Aureobasidium vel aff.	Arx & Müller (1975), Hermanides-Nijhof (1977)
1.1.	Mycosphaerella abietis Lind.	
	= Toxosporium camptospermum (Pk.) Maub.	Grove (1937), Sutton (1975)
2.3.1.	M. aegopodii Pot.	
	= Phloeospora aegopodii Gr.	
	= Phyllosticta aegopodii All.	Potebnia (1910)
	M. aleuritidis (Miyake) Ou	
	= Cercospora aleuritidis Miyake	

2.3.1.	M. arachidis Deighton = Cercospora arachidicola Hori	Mulder & Holliday (1974)
2.3.1.	M. arachnoidea Wolf = Cercospora arachnoidea Wolf	Wolf (1936)
	M. areola Ehrl. & Wolf = Septocylindrium gossypii (Speg.) Subram.	Ehrlich & Wolf (1932), Subramanian (1971)
2.3.1.	M. aronici Volk = Passalora aronici (Fckl.) Arx	Arx (1950)
2.3.1.	M. ascophyllii Cotton = Septoria vel aff.	Webber (1967)
2.3.1.	M. aurea Stone = Septoria aurea Ell. & Ev.	Stone (1916)
2.2.1.	M. bellona Sacc. = Phyllosticta pyrina Sacc.	Grove (1935)
2.3.1.	M. berkeleyi W.A. Jenk. = Cercosporidium personatum (B. & C.) Deight.	Mulder & Holliday (1974)
	M. bolleana Higgins = Cercospora bolleana (Thüm.) Speg.	Higgins (1920)
2.3.1.	M. brassicicola (Duby) Lindau = Asteromella brassicae Boerema & van Kest.	Grove (1935), Dring (1961), Punithalingam & Holliday (1975)
	M. caryigena Dem. & Cole = Cercosporella caryigena (Ell. & Ev.) Höhn.	fide ATCC & C.B.S. catalogue
	M. ceptis (Schw.) House = Septoria ceptidis Berk. & Curt.	
2.3.1.	M. cerasella = Cercospora sp.	Klebahn (1918)
2.3.1.	M. cercidicola (Ell. & Kellerm.) Wolf = Cerecospora cercidicola Ell.	Wolf (1940)
	M. chamaenerii Saville = Ramularia chamaenerii Rostr.	
	M. citri Whiteside = Stenella sp.	Sivanesan & Holliday (1976)
2.1.	M. citrullina Gross. = Ascochyta citrullina Smith	Grove (1935)
2.3.1.	M. confusa Wolf = Cercospora rubi Sacc.	Wolf (1935,1936)
2.2.1.	M. coptis (Schw.) House = Septoria coptis Berk. & Curt.	Barr (1972)
2.2.1.	M. cornicola Tehon & Daniels = Phoma sp.	Tehon & Daniels (1925)
2.3.1.	M. cruenta Latham = Cercospora cruenta Sacc.	Latham (1934), Ellis (1976)
	M. cucumis (Fautr. & Roum.) Chiu. & Walker = Ascochyta cucumeris Fautr. & Roum.	Moore (1959)
	M. dalbergiae Müller & Ahmad. = Cercospora sissoo Syd.	
2.3.1.	M. davisii Jones = Cercospora davisii Ell. & Ev.	Jones (1944)
2.2.2.	[?] M. dearnessii Barr = Lecanosticta acicola (Thüm.) Syd.	Barr (1972)
2.3.1.	M. dianthi (Burt.)Jørstad = Cladosporium echinulatum (Burt.) de Vries	Vries (1952), Ellis (1971)
2.3.1.	M. digitalis-ambiguae Arx = Asteromella digitalis-ambiguae Arx = Ramularia digitalis-ambiguae Arx	Arx (1949)
2.	M. ebulina Petr. = Ramularia [?] sambucina Sacc.	Petrak (1915)

2.2.4.	M. effigurata (Schw.) House	
	= Asteromella fraxini (Berk. & Curt.) Petr.	
	= Marssonia fraxini Ell. & Davis	
	= Piggotia fraxini Berk. & Curt.	
	= Stictochorella fraxini (B. & C.) Höhn.	Wolf & Davidson (1941), Shaw (1973)
2.3.1.	M. fijiensis Morelet	
	= Cercospora sp.	Meredith & Lawrence (1969), Mulder & Holliday (1974)
	M. fragariae (Tul.) Linder	
	1.1. = Phyllosticta fragariicola Desm. & Rob.	
	2.3.1. = Ramularia brunnea Pk.	
	1.1. = Ramularia tulasnei Sacc.	Klebahn (1918), Grove (1935), Barr (1972)
2.2.2.	M. fraxinicola (Schw.) House	
	= Phyllosticta viridis Ell. & Kell. (= Asteromella sp. fide DiCosmo)	Wolf (1939)
2.2.2.	M. graminicola (Fuckel) Sanderson	
	= Septoria tritici Rob. apud Desm.	Sanderson (1976)
1.1.	M. grossulariae (Auersw.) Lindau	
	= Septoria ribis Desm.	
	= [?] Phyllosticta grossulariae Sacc.	Grove (1935), Shear (1943)
	M. hedericola (Desm.) Lindau	
	= Septoria hederae Desm.	Moore (1959)
2.3.1.	M. hermoine Sacc.	
	= Phyllosticta helleborella Sacc.	Grove (1935)
1.1.	M. heucherae (Ell. & Ev.) Petr.	
	= Phyllosticta heucherae Ell. & Ev.	Barr (1972)
2.2.1.	M. impatientis (Pk. & Clinton) House	
	= Septoria sp.	Barr (1972)
1.1.	M. iridis (Desm.) Schröt. apud Cohn	
	= Cladosporium gracile Wallr.	Barr (1972)
2.1.	M. isariphora Johans.	
	= Septoria stellariae Rob. & Desm.	Fuckel (1870), Grove (1935)
1.1.	M. janus (B. & C.) Petr.	
	= Asteromella castanicola (Ell. & Ev.) Petr.	Barr (1972)
	M. joerstadii Arx	
	= Septoria rubi (Duby) Westend	Arx (1957)
1.1.	M. juncaginacearum Schrot.	
	= Asteroma juncaginacearum Rabenh.	Grove (1937)
2.2.4.	M. killiani Petr.	
	= Placosphaeria trifolii (Pers. ex Fr.) Trav.	
	= Polythrincium trifolii Schm. & Kunze ex Fr.	Bayliss-Elliot & Stansfield (1924), Wolf (1935), Barr (1972)
2.3.1.	M. lapathi (Laibach) Petr.	
	= Ramularia obovata Fckl.	Laibach (1921), Barr (1968)
	M. latebrosa (Cke.) Schröt.	
	= Septoria aceris (Lib.) B. & Br.	
2.3.1.	M. lethalis Stone	
	= Ascochyta lethalis Ell. & Barth.	
	= Ascochyta meliloti (Trel.) Davis	Stone (1912)
1.1.	M. ligea Sacc.	
	= Septoria rubi Westd.	Grove (1935)
	M. ligulicola Baker et al.	
	= Aschochyta chrysanthemi Stev.	
1.1.	M. ligustri Fckl.	
	= Phyllosticta ligustri Sacc.	
	= Septoria ligustri Kickx.	Grove (1935)
1.1.	M. linorum (Wr.) Gracia-Rad	
	= Septoria linicola (Spg.) Gar.	Shaw (1973)

2.3.1.	M. macrospora (Kleb.) Jørstad = Cladosporium iridis (Fautr. & Roum.) de Vries	de Vries (1952), Ellis (1971)
2.2.2.	M. maculiformis Schröt. = Phyllosticta betulina Sacc. = Phyllosticta maculiformis Sacc.	
	2.3.1. = Ramularia sp. = Septoria quercina Desm.	Shear (1921), Overholts (1929), Grove (1935)
2.1.	"M. maculiformis Schröt. var. castaneicola" = Septoria castaneicola Desm.	Grove (1935)
2.1.	M. maculiformis Schröt. var. hippocastani Jaap. = Septoria hippocastani B. & Br.	Grove (1935)
2.3.1.	M. martagonis Arx = Cercosporella hungarica Baumler	Arx (1949)
2.1.	M. melaena Sacc. = Phoma melaena Mont. & Dur.	
2.3.1.	M. milleri Hodges & Haasis = Phaeoisariopsis magnoliae (Ell. & Harkn.) Jong & Morris	Hodges & Haasis (1964)
2.3.1.	M. musicola Leach = Cercospora musae Zimm.	Meredith & Lawrence (1970), Mulder & Holliday (1974)
	M. nigro-maculans Shear apud Shear, Stevens & Bain = Ramularia nigro-maculans Shear	Shaw (1973)
	M. occulta Bub. = Phyllosticta occulta Bub.	Bubak (1915)
	M. oxyacanthae Jaap = Phloeospora oxyancanthae Wall.	
2.3.1.	M. persica Higgins & Wolf = Cercosporella persica Sacc.	Higgins & Wolf (1937)
	M. pinodes (Berk. & Blox. in B. & Br.) Vest. = Ascochyta pinodes Jones = Ascochyta pisi Lib.	Moore (1959), Shaw (1973)
	M. piri (Auersw.) Boer. = Septoria piricola Desm.	
2.3.1.	M. platanifolia Cke. = Cercospora platanifolia Ell. & Ev.	Wolf (1938), Barr (1972)
1.1.	M. polygramma Johans. & Magn. = Phoma polygramma Sacc.	Grove (1935)
1.1.	M. populi Schröt. = Septoria populi Desm.	Grove (1935)
2.3.1.	M. populicola Thom. = Septoria populicola Pk.	Thompson (1941)
2.3.1.	M. populorum Thom. = Septoria musiva Pk.	Thompson (1941), Barr (1972)
	M. pruni-persicae Deighton = Miuraea persica (Sacc.) Hara	Deighton (1967)
2.3.1.	M. pseudomaculaeformis (Desm.) Schröt. = Ovularia bulbigera (Fckl.) Sacc. = Ramularia sp.	Arx (1949), Barr (1972)
	M. psilospora Gilm. & Wadl. = Septoria querceti Thüm.	
2.3.1.	M. punctiformis (Pers. ex Fr.) Starb. = Ramularia sp.	Klebahn (1918), Barr (1972)
	M. rabiei Kov. = Ascochyta rabiei (Pass.) Labr.	
2.3.1.	M. ribis (Fckl.) Feltg. = Septoria ribis Desm.	Klebahn (1918), Grove (1935), Shear (1943)
2.3.1.	M. rosicola B.H. Dav. ex Deight. = Cercospora rosicola Pass.	Davis (1938), Deighton (1967)

2.3.1.	M. rubi Roark = Septoria rubi West.	Roark (1921), Demaree & Wilcox (1943)
1.1.	M. rubina (Pk.) Jacz. = Phoma sp.	Zeller (1927)
1.1.	M. selene Sacc. = Phyllosticta oxalidis Sacc.	Grove (1935)
2.2.2.	M. sentina (Fr.) Schröt. = Septoria piricola Desm.	Klebahn (1908), Grove (1935), Shaw (1973)
2.3.1.	M. stigmina-platani Wolf = Stigmina platani (Fckl.) Sacc.	Wolf (1938), Barr (1972)
2.3.1.	M. superflua (Fckl.) = Phoma superflua Sacc. = Septocylindrium urticae (Ces.) Subram.	Grove (1935), Arx (1949), Subramanian (1971)
	M. tabifica (Prill. & Del.) Lindau = Phoma betae Frank = Ramularia sp.	Grove (1935), Shaw (1973)
2.3.1.	M. tassiana (de Not.) Johans. = Cladosporium herbarum (Pers.) Link	Arx (1950), Barr (1958,1972)
2.3.1.	M. tecomae Wolf = Cercospora sordida Sacc.	Wolf (1943)
	M. tinosporae Ajr. & Mund. = Cercosporella tinosporae (Lacy & Thirum.) Deighton	
2.3.1.	M. tulasnei (Jancz.) Lindau in Lafar = Cladosporium herbarum (Pers.) Fr.	Ruehle (1931), Arx (1950)
	M. tulipiferae (Schw.) Higgins = Asteromella sp. ([?] spermatial fide DiCosmo ined.) = Cercospora lirodendri Ell. & Hark.	Higgins (1936)
2.2.2.	M. ulmi Kleb. = Cylindrosporella inconspicua (Cav.) Arx = Phyllosticta bellunensis Mart. = Septogloeum ulmi Died.	Grove (1935), Arx (1978)
	M. umbrosa Sacc. = Phyllosticta galeopsidis Sacc.	Grove (1935)
	Mycosphaerella sp. = Cercoseptoria sp. = Fusicladiella sp.	Höhnel (1919), Arx (1975)
	Mytilidion karstenii Sacc. = Septonema sp.	Lohman (1933)
2.3.1.	M. scolecosporum Lohm. = Septonema toruloideum Cke. & Ell.	Lohman (1932,1933)
2.2.4.	Neoparodia ekmanii Petr. & Cif. = Chuppia vel aff. = Sarcinella vel aff.	Petrak & Ciferri (1932), Arx & Müller (1975)
	[?] Omphalospora sp. (? = Plectosphaerina Kirschst. fide Petrak = Ascospora Fr. nom. confusum fide Ainsworth et al. (1971)) = Hendersonia rubi (West.) Sacc. = Seimatosporium foliicola (Berk.) Shoem.	Zeller (1927), Ainsworth et al. (1971), Sutton (1975)
2.2.4.	Ophiobolus acuminatus (Sow. ex Fr.) Duby apud Rabenh. = [?] Coniothyrium sp.	Shoemaker (1976)
2.1.	O. cirsii Sacc. = Rhabdospora cirsii Karst.	Grove (1935), Wehmeyer (1946)
2.3.1.	O. drechsleri Shoemaker = unnamed pycnidial coelomycete (? = Asteromella vel aff. fide DiCosmo) = unnamed hyphomycete with proliferating phialides	Drechsler (1934), Shoemaker (1976)

2.3.1.	O. fulgidus (Clint. & Peck apud Peck) Sacc.	
	= Phoma vel aff.	Drechsler (1934)
2.3.1.	O. graminus (Sacc.) Sacc.	
	= microconidia produced from ascospores	Weste (1972)
2.3.1.	O. herpotrichus (Fr.) Sacc.	
	= Acremonium alternatum Link	
	= Septoria sp.	
	= Urohendersoniella sp.	Voges (1914), Drechsler (1934), Webster & Hudson (1957), Wehmeyer (1975)
2.2.2.	Ophiocapnocoma batistae Hughes	
	= Capnophialophora sp.	Hughes (1967)
2.2.2.	O. phloiophila (Fisher) Hughes	
	= Capnophialophora sp.	
	= Hormiokrypsis libocedri Bat. & Nasc.	Hughes (1967)
2.2.2.	Ophiocapnocoma sp.	
	= Capnocybe sp.	
	= Capnophialophora sp.	
	= Hormiokryopsis sp.	Hughes (1972), Arx & Müller (1975)
	= Torulopsis sp.	
2.2.1.	Ophioparodia pulchra Petr. & Cif.	
	= Septoidium sp.	Petrak & Ciferri (1932)
1.1.	Otthia amica Sacc., Bomm. & Rouss.	
	= Hendersonia diplodioides Ell. & Ev.	Shaw (1973)
2.1.	O. crataegi Fckl.	
	= Diplodia crataegi Westd.	
	= Phoma crataegi Sacc.	Grove (1935)
2.3.1.	O. spiraeae (Fckl.) Fckl.	
	= Diplodia sarmentorum (Fr.) Fr.	Booth (1958)
2.3.1.	Otthia sp.	
	= Stigmina sp.	Müller (1971)
1.1.	Paranectriella juruana (P. Henn.) Piroz.	
	= Titaea sp.	Pirozynski (1976)
2.3.1.	Paraphaeosphaeria michotii (Westend) O. Eriks.	
	= Coniothyrium scirpi Trail	Webster (1955), Müller (1973)
2.3.1.	P. obtusispora (Speg.) O. Erikss.	
	= Coniothyrium sp.	Lucas (1963), Müller (1973)
2.3.1.	P. rusci (Wallr.) O. Erikss.	
	= Coniothyrium sp.	Brefeld (1891), Müller (1973)
	Parodiellina manaosensis (P. Henn.) Arnaud	
	= Arnaudia manaoensis (P. Henn.) Arn.	Kendrick & Carmichael (1973)
2.2.4.	Perisporiopsis sp. (sub Parodiopsis hurae (Arn.) Baker & Dale)	
	= Septoidium sp.	Hansford (1946), Baker & Dale (1951), Ellis (1971), Arx & Müller (1975)
	Phaeocryptopus sp.	
	= Rhizophoma pini (Desm.) Petr. in Syd.	Ainsworth et al. (1971)
	Phaeocryptopus sp.	
	= Rhizosphaera kalkhoffi Bub.	Ainsworth et al. (1971)
2.2.1.	Phaeosphaeria bambusae Miyake & Hara	
	= [?] Phyllosticta sp.	Tanaka (1922)
2.3.1.	P. fuckelii (Niessl) Holm	
	= Phaeoseptoria sp.	Webster & Hudson (1957), Müller (1973)
2.3.1.	P. microscopica (Karst.) O. Erikss.	
	= Phaeoseptoria sp.	Webster (1955), Müller (1955)
2.3.1.	P. nigrans (Rob. ex Desm.) Holm	
	= Septoria alopecuri Syd.	Hughes (1949), Müller (1973)
2.3.1.	P. nodorum (Müller) Hedj.	
	= Hendersonia nodorum (Berk.) Petr.	Lucas & Webster (1967), Müller (1973)

2.2.1.	P. oryzae Miyake	
	= Phyllosticta sp.	Tanaka (1922)
2.3.1.	P. tritici (Garo) Hedj.	
	= Hendersonia sp.	Webster & Hudson (1957), Müller (1973)
2.3.1.	P. typharum (Desm.) Holm	
	= Hendersonia typhae Oud.	Webster (1955), Müller (1973)
2.2.4.	Phragmocapnias Theiss. & Syd.	
	= Conidiocarpus sp.	Hughes (1976)
1.1.	Pilgeriella sp.	
	= Septoidium sp.	Arx & Müller (1975)
1.1.	Platychora ulmi (Schl. ex Fr.) Petr., sub Dothidella ulmi (Schl. ex Fr.) Winter	
	= Piggotia asteroidea Berk. & Br.	
	= Placosphaeria ulmi Gr.	Grove (1935,1937)
2.2.2.	Pleospora bjorlingii Byford	
	= Phoma betae Frank	Byford (1963), Booth (1967)
2.3.1.	P. calvescens (Fr. ex Desm.) Tul.	
	= Helminthosporium papaveris Henn.	
	= Microdiplodia henningsii Staritz	Webster & Lucas (1959), Moore (1959)
2.3.1.	P. cytisi Fckl.	
	= Leptophoma sp.	
	= Phoma sp.	Wehmeyer (1975)
	P. flavo-fusca	
	= Alternaria sp.	
	= Phoma sp.	Wehmeyer (1975)
2.3.1.	P. herbarum (Pers. ex Fr.) Rabenh.	
	= Phoma herbarum Westd.	
	= Stemphylium botryosum Wallr.	Grove (1935), Wehmeyer (1961), Webster & Lucas (1961), Simmons (1969)
	P. herbarum (Pers. ex Fr.) Rabh. f. lactucum Pad. & Snyd.	
	= Stemphylium botryosum Wallr. f. lactucum Pad. & Snyd.	
	P. infectoria Fckl.	
	= Alternaria sp.	Wehmeyer (1948), Simmons (1969)
2.3.1.	P. inverecunda (de Not.) Ces.	
	= Stagnosopora opuntiae Tassi	Lucas (1965), Wehmeyer (1975)
1.1.	P. leguminum Rabenh.	
	= Phoma leguminum Westd.	Grove (1935)
2.3.1.	P. mali Hesler	
	= Hendersonia mali Thüm.	Hesler (1927)
2.3.1.	P. media Niessl	
	= Camarosporium [?] punctiforme (Sacc.) Höhn.	Webster & Lucas (1961)
	P. orbicularis Auersw.	
	= Alternaria sp.	
	= Phoma sp.	Wehmeyer (1975)
	P. papaveracea (de Not.) Sacc.	
	= Dendryphion penicillatum (Corda) Fr.	Ellis (1971)
	P. rubicunda Niessl	
	= Phoma sp.	Wehmeyer (1975)
2.3.1.	P. scirpicola (DC.) Karst.	
	= Alternaria sp.	Lucas & Webster (1964), Ellis (1976)
	P. scrophulariae (Desm.) Höhn.	
	= Alternaria sp.	
	= Phoma sp.	Wehmeyer (1975)
	P. shepherdiae Pk.	
	= Coniothyrium sp.	Wehmeyer (1975)
2.3.1.	P. spartium-juncei E. Müller	
	= Coniothyrium sp.	Müller (1957)
2.3.1.	P. triglochinicola Webster	
	= Stemphylium triglochinicola Sutton & Piroz.	Webster (1969)

2.3.1.	P. typhicola (Cke.) Sacc.	
	= Phoma [?] typharum Sacc.	Webster & Lucas (1959)
2.3.1.	P. vagans Niessl	
	= Hendersonia sp.	Webster (1955)
2.3.1.	P. valesiaca (Niessl) Müller	
	= Alternaria sp.	Lucas & Webster (1964), Ellis (1971)
2.3.1.	P. vitalbae (de Not.) Berl.	
	= Hendersonia sp.	Webster & Lucas (1961)
2.2.1.	P. vulgaris Niessl	
	= Phoma oleracea Sacc.	
	= Phoma vulgaris Sacc.	Grove (1935)
2.3.1.	Pleospora spp. indet.	
	= Stemphylium globuliferum (Vestr.) Simm.	
	= S. majusculum Simm.	
	= S. triglochinicola Sutt. & Piroz.	
	= S. vesicarium (Wallr.) Simm.	Simmons (1969)
2.3.1.	Plowrightia ribesia Sacc.	
	= Aureobasidium vel aff.	
	= [?] Hormonema vel aff.	
	= Rabenhorstia ribesia Cke. & Masse	Grove (1935), Tubaki (1958), Hermanides-Nijhof (1977)
2.2.2.	Podonectria aurantii (Höhn.) Petch	
	= Tetracrium aurantii P. Henn.	Rossman (1978)
2.2.2.	P. bambusicola (Rehm.) Piroz.	
	= Tetracrium sp.	Pirozynski (1976), Rossman (1978)
2.2.2.	P. coccicola (Ell. & Ev.) Petch	
	= Tetracrium coccicolum Höhn.	Höhnel (1911), Rossman (1978)
2.2.1.	P. coccorum (Petch) Rossman	
	= Peziotrichum lachnella (Sacc.) Lind.	
	= Volutella epicoccum Petch	Petch (1927), Rossman (1978)
2.2.2.	P. echinata Petch	
	= Tetracrium echinatum Petch	Petch (1921), Rossman (1978)
2.2.2.	P. gahnia Dingley	
	= Tetranacrium sp.	Dingley (1954), Rossman (1978)
2.3.1.	Preussia aemulans (Rehm.) Arx	
	= Phoma vel aff.	Arx (1973)
2.3.1.	P. cylindrica Malloch & Cain	
	= [?] Phoma sp.	Malloch & Cain (1972)
2.3.1.	P. dispersa (Clum) Cain	
	= Phoma vel aff.	Cain (1961)
2.2.4.	Prillieuxina winteriana (Pazschke) Arn.	
	= Leprieurina winteriana Arnaud	Orton (1924)
2.3.1.	Pringsheimia chamaecyparis Froid.	
	= Dothichiza vel aff.	Froidevaux (1972)
	Pringsheimia spp.	
	= Hormonema spp.	Hermanides-Nijhof (1977)
2.3.1.	Protocucurbitaria ribicola Naumov	
	= Plenodomus sp. (Phoma vel aff.)	Müller (1963)
2.3.1.	Pseudocochliobolus nisikadoi Tsuda, Ueyama & Nishihara	
	= Helminthosporium coicis Niski.	Tsuda, Ueyama & Nishihara (1977)
2.2.2.	Puttemansia sp.	
	= Guelichia sp.	
	= Spermatoloncha sp.	
	= Tetracrium sp.	
	= Titaea sp.	Höhnel (1911), Kendrick & Carmichael (1973), Pirozynski (1976)
2.2.2.	Pycnothyrium perexiguum (Speg.) Arx	
	= Leptothyrium vulgare (Fr.) Sacc.	Arx (1964), Arx & Müller (1975)
2.3.1.	Pyrenophora alternarina Whitehead & Dickson	
	= Alternaria sp.	Whitehead & Dickson (1952)
2.3.1.	P. bromi (Rab. ex Schlecht.) Shoem.	
	= Drechslera bromi (Died.) Shoem.	Drechsler (1923), Ellis (1971)

2.3.1.	P. chaetomoides Speg. (= P. avenae Ito & Kurib. fide Ainsworth et al.)	
	= Drechslera avenacea (Curt. ex Cke.) Shoem.	Ainsworth et al. (1971), Ellis & Waller (1973)
2.3.1.	P. dictyoides Paul & Parb.	
	= Corynespora vel aff.	
	= Drechslera dictyoides (Drechs.) Shoem.	Paul & Parbery (1968)
2.3.1.	P. erythrospila Paul	
	= Drechslera erythrospila Paul	Shoemaker (1959), Paul (1972)
2.3.1.	P. graminea Ito & Kuribayashi apud Ito	
	= Drechslera graminea (Rab. ex Schlecht.) Shoem.	Ellis & Waller (1973)
2.3.1.	P. japonica Ito & Kurib.	
	= Drechslera tuberosa (Atk.) Shoem.	Shoemaker (1959), Ellis (1971)
2.3.1.	P. lolii Dov.	
	= Helminthosporium sp.	Dovaston (1948)
2.3.1.	P. phaeocomes (Fr.) Rebent.	
	= Drechslera sp.	Graham (1955)
	P. scirpi (Rab.) Wehm.	
	= Alternaria sp.	Wehmeyer (1975)
	P. scirpicola (DC. ex Fr.) Müller	
	= Helminthosporium sp.	Müller (1951), Arx (1974)
2.3.1.	P. secalis Whitehead & Dickson	
	= Drechslera tuberosa (Atk.) Shoem.	Whitehead & Dickson (1952), Shoemaker (1959)
2.3.1.	P. seminiperda (Brittl. & Adam) Shoem.	
	= Drechslera verticillata (O'Gara) Shoem.	
	= unnamed pycnidial coelomycete (? = Asteromella vel aff. fide DiCosmo)	Brittlebank & Adam (1924), Shoemaker (1966), Paul (1969)
2.3.1.	P. teres Drechsler	
	= Drechslera teres (Sacc.) Shoem.	Webster (1951), Ellis & Waller (1973)
2.3.1.	P. tetrarrhenae Paul	
	= Drechslera tetrarrhenae Paul	Paul (1971)
2.3.1.	P. trichostoma (Fr.) Ces. & de Not.	
	= Drechslera teres (Sacc.) Shoem.	Webster (1951)
2.3.1.	P. tritici-repentis (Died.) Drechs.	
	= Drechslera tritici-repentis (Died.) Shoem.	Shoemaker (1959), Ellis & Waller (1976)
	P. typhaecola (Cke.) Sacc.	
	= Phoma sp.	Wehmeyer (1975)
	Questieria sp.	
	= Questieriella sp.	Ainsworth et al. (1971), Arx & Müller (1975)
2.3.1.	Rhopographus zeae Pat.	
	= Clasterosporium longisporum Voor.	Voor hees (1934)
2.2.2.	Rhytidenglerula carnea (Ell. & Mart.) Höhn.	
	= Capnodiastrum sp.	Barr (1972)
2.3.1.	Rhytidiella baranyayi Funk & Zalasky	
	= unnamed phialidic coelomycete	Funk & Zalasky (1975)
2.3.1.	R. moriformis Zalasky	
	= Phaeoseptoria sp.	Zalasky (1968)
1.1.	Schiffnerula mirabilis Höhn.	
	= Mitteriella sp.	
	= Sarcinella sp.	Arx & Müller (1975)
2.2.4.	S. pulchra (Sacc.) Petr.	
	= Sarcinella heterospora Sacc.	Ellis (1971)
2.2.2.	Scirrhia acicola (Dearness) Siggers	
	= Lecanosticta acicola (Thüm.) Syd.	Barr (1972)
2.2.4.	S. insculpta (Wallr.) Barr	
	= Asteromellopsis insculpta Hess & Müller	Hess & Müller (1951), Barr (1972)
2.3.1.	S. pini Funk & Parker	
	= Dothiostroma pini Hulb.	Funk & Parker (1966)

2.3.1.	S. rimosa (Alb. & Schw. ex Fr.) Fckl.	
	= Acremonium vel aff.	
	= Hadrotrichum phragmites Fckl.	
	= Phoma rimosa Westd.	Grove (1935), Obrist (1959), Barr (1972)
2.3.1.	Schizothyrium pomi (Mont. ex Fr.) Arx	
	= Zygophiala jamaicensis Mason	Baker et al. (1977)
1.1.	S. ptarmicae Desm.	
	= Leptothyrium ptarmicae Sacc.	Grove (1937)
2.2.4.	Scorias cylindrica Yam.	
	= Scolecoxyphium sp.	Yamamoto (1954), Hughes (1976)
2.2.4.	S. philippinensis Mendoza	
	= Scolecoxyphium sp.	Hughes (1976)
2.2.4.	S. spongiosa (Schw.) Fr.	
	= Polychaeton sp.	Hughes (1976)
2.3.1.	Setosphaeria holmii (Lutt.) Leon & Suggs	
	= Exserohilum holmii (Lutt.) Leon & Suggs	Leonard & Suggs (1974)
2.3.1.	S. pedicellata (Nels.) Leon. & Suggs	
	= Exserohilum pedicellatum (Henry) Leon. & Sugg	Leonard & Suggs (1974)
2.3.1.	S. prolata Leon. & Suggs	
	= Exserohilum prolatum Leon. & Suggs	Leonard & Suggs (1974)
2.3.1.	S. rostrata Leon.	
	= Exoserohilum rostratum (Drechs.) Leon. & Suggs	Leonard (1976)
2.3.1.	S. turcica (Lutt.) Leon. & Suggs	
	= Exoserohilum turcicum (Pass.) Leon. & Suggs	Leonard (1976)
2.2.4.	Seuratia globifera (Ell. & Ev.) Meeker	
	= Myriophysella chilensis Speg.	Meeker (1975)
2.2.4.	S. maunauluana Meeker	
	= Atichia sp.	Meeker (1975)
2.2.4.	S. millardetii (Racib.) Meeker	
	= Atichia glomerulosa (Ach. ex Mann.) Stein	Meeker (1975)
2.3.1.	Sphaerulina oryzina Hara	
	= Cercospora oryzae Miyake	Deighton (1967), Barr (1972)
1.1.	S. rehmiana Japp.	
	= Asteromella vel aff. (microconidial)	
	= Cercospora sp.	
	= Septoria rosae Desm. (Phloeospora rosae rosae (Desm.) Höhn.	Grove (1935), Barr (1972), Arx & Müller (1975)
2.2.2.	S. rubi Dem. & Wilcox	
	= Asteromella vel aff. (microconidial)	
	= Septoria sp. (Cylindrosporium rubi Ell. & Morg.)	Barr (1972), Shaw (1973)
2.2.2.	S. taxi (Cke.) Masse	
	= Cytospora taxifolia Pilát & Macal	Callen (1938), Shaw (1973)
2.2.4.	Strigopodia batistae Hughes	
	= Antennatula sp.	Hughes (1968), Barr (1972), Ellis (1976)
2.2.4.	S. resinae (Sacc. & Bres.) Hughes	
	= Antennatula sp.	
	= Capnophialophora sp.	Hughes (1970), Ellis (1971), Barr (1972), Arx & Müller (1975)
2.3.1.	Sydowia dothideoides Dearn. & Barth.	
	= Hormonema sp.	
	= [?] Dothichiza sp.	Shear & Davidson (1940), Barr (1972)
2.3.1.	S. polyspora (Bref. & Tav.) Müller	
	= Hormonema dematioides Lagerberg & Melin	
	= Sclerophoma magnusiana Wilson & Hahn	
	= Sclerophoma pithyophila (Corda) Höhn.	Butin (1964), Smerlis (1970), Hermanides-Nijhof (1977)

1.1.	Teratosphaeria sp.	
	= [?] Dendrophoma sp.	Luttrell (1973), Wehmeyer (1975)
2.3.1.	Thaxteriella pezicula (B. & C.) Petr.	
	= Helicoma muelleri Corda	Pirozynski (1972)
2.2.4.	Thyridaria rubro-notata (Berk. & Br.) Sacc.	
	= Cytoplea juglandis (Schum.) Petr.	Chesters (1938)
2.2.4.	Thyriopsis halepensis (Cke.) Theiss. & Syd.	
	= unnamed pycnidial coelomycete [?] spermatial	Ouellette (1966)
1.1.	Trabutia quercina (Fr. & Rud.) Sacc. & Roum.	
	= Coniella sp. (sub Baeumleria)	Ainsworth et al. (1971), Arx & Müller (1975)
1.1.	Trematosphaeria sp.	
	= Phoma sp.	Arx & Müller (1975)
2.3.1.	Trichometasphaeria gallica E. Müller	
	= [?] Ascochyta sp.	Müller (1957)
2.2.4.	Trichopeltheca asiatica Bat., Costa & Cif.	
	= Plokamidomyces colensoi Bat., Costa & Cif.	
	= Trichothallus sp.	Hughes (1965)
2.2.4.	T. stevensii Hughes	
	= Plokamidomyces sp.	
	= Trichothallus hawaiiensis Stev.	Stevens (1925), Hughes (1965)
2.2.4.	Trichothyrium asterophorum (B. & Br.) Höhn.	
	= Isthmospora spinosa Stev.	Hughes (1953)
2.2.4.	T. hansfordii Hughes	
	= Hansfordiella meliolae (Hans) Hughes	Hughes (1951,1953)
1.1.	Triposporiopsis spinigera (Höhn.) Yamamoto	
	= Tripospermum sp.	Arx & Müller (1975), Hughes (1976)
2.3.1.	Tryblidiella hysterina (Duf.) Shear	
	= Diplodia sp.	Shear (1933)
2.3.1.	T. leprieuri (Mont.) Sacc.	
	= Diplodia sp.	Shear (1933)
2.3.1.	T. rufula (Spreng) Sacc.	
	= Diplodia sp.	Shear (1933)
2.2.4.	Tubeufia cerea (B. & C.) Booth	
	= Helicosporium vegetum C.G. Nees	Ellis (1971)
2.2.4.	T. helicoma (Phil. & Plowr.) Piroz.	
	= Helicosporium pannosum (B. & C.) Moore	Pirozynski (1972)
2.3.1.	T. padulosa (Crouan & Crouan) Rossman	
	= Helicosporium phragmitis Höhn.	Höhnel (1909), Webster (1951), Rossman (1977)
2.2.1.	Uleothyrium amazonicum Petr.	
	= Septothyrella uleana Syd.	Arx & Müller (1975)
2.3.1.	Venturia acerina Plak. ex Barr	
	= Cladosporium humile J.J. Davis	Plakidas (1942), Barr (1968), Ellis (1976)
2.3.1.	V. asperata Sam. & Sivan.	
	= Fusicladium sp.	Samuels & Sivanesan (1975)
2.3.1.	V. carpophila E.E. Fisher	
	= Fusicladium carpophilum (Thüm.) Oudem.	Fisher (1961), Ellis (1971)
2.2.2.	V. crataegi Aderh.	
	= Fusicladium vel aff.	Hughes (1953)
2.2.2.	V. cerasi Aderh.	
	= Fusicladium cerasi (Rabh.) Sacc.	Hughes (1953)
2.3.1.	V. chlorospora (Ces.) Karst.	
	= Fusicladium sp.	Müller & Arx (1962)
2.2.2.	V. ditricha (Fr.) Karst.	
	= Fusicladium betulae (Rob. & Desm.) Aderh.	Barr (1968)
2.2.2.	V. inaequalis (Cke.) Wint.	
	= Spilocaea pomi Fr. ex Fr.	Barr (1968), Ellis (1971)
2.2.2.	V. macularis (Fr.) Müller & Arx	
	= Pollaccia radiosa (Lib.) Bald. & Cif.	Barr (1968)

2.2.2.	V. pirina (Bref.) Aderh.	
	= Fusicladium virescens Bon.	Hughes (1953), Barr (1968)
2.3.1.	V. populina (Vuill.) Fabric.	
	= Pollaccia elegans Servassi	Barr (1968), Ellis (1976)
2.2.2.	V. saliciperda Nuesch.	
	= Pollaccia saliciperda (All. & Tub.) Arx	Barr (1968)
2.2.2.	V. syringae (Syd.) Barr	
	= Fusicladium sp.	Barr (1968)
2.2.2.	V. tremulae Aderh.	
	= Pollaccia radiosa (Libert) Bald. & Cif.	Ainsworth et al. (1971)
2.2.2.	V. turfosorum Mouton	
	= Fusicladium sp.	Barr (1968)
2.2.1.	Vizella hendrickxii (Hansf.) Hughes	
	= Manginula [?] perseae Arn.	Hughes (1953)
2.2.4.	V. oleariae Swart	
	= Manginula sp.	Swart (1971)
	Xenodium petrakii Syd.	
	= Xenodiella petrakii Syd.	Sydow (1935)
2.3.1.	Xenomeris abietis Barr	
	= Hormonema dematioides Lagerb. & Melin.	Sydow (1935), Funk & Shoemaker (1971)
2.2.4.	Yamamotoa carludovicae (Bat.) Arx & Müller	
	= [?] Clasterosporium sp.	
	or Mitteriella sp.	
	or Sarcinella sp.	Arx & Müller (1975)

TELEOMORPH-ANAMORPH CONNECTIONS

ALPHABETICALLY BY BITUNICATE ASCOMYCETE ORDER AND FAMILY

INDICATING NUMBER OF CONNECTIONS IN EACH DEUTEROMYCETE GENUS

Dothideales

Capnodiaceae

Achaetobotrys Bat. & Cif.
= Antennariella (2)

Acrogenotheca (Fraser) Cif. and Bat.
= unnamed coelomycete (pycnidial) (1)

Aithaloderma Syd.
= Ciferrioxyphium (2)
(see Hughes (1976) pp. 737, 758)
= Microxiphium (1)
= unnamed coelomycete (pycnidial) (3)

Antennulariella Woron.
= Antennariella (1)
= Capnodendron (1)
= Microxiphium (1)

Brooksia Hansf.
= Hiospira (1)
= Capnogoniella (1)

Capnodium Mont.
= Fumagospora (1)
= Phaeoxyphiella (1)
= Scolecoxyphium (2)

[?] Dennisiella Bat. & Cif.
= Microxiphium (2)
(see Hughes (1976) for important discussion
on familial affinities of Dennisiella)

Euantennaria Speg.
= Antennatula (4)
= Hormisciomyces (4)

Laterotheca Bat.
= unnamed coelomycete (pycnidial) (1)
= unnamed synnematous hyphomycete (1)

Limacinia Neger
= Capnocybe (5)
= Capnophialophora (4)

Limacinula (Sacc.) Höhn.
= ascospores w. conidiogenous cells (1)

Metacapnodium Speg.
= Capnobotrys (1)
= Capnocybe (1)
= Capnophialophora (1)
= Capnosporium (1)

Ophiocapnocoma Bat. & Cif.
= Capnocybe (1)
= Capnophialophora (3)
= Hormiokrypsis (2)
= Torulopsis (1)

Phragmocapnias Theiss. & Syd.
= Conidiocarpus (1)

Scorias Fr.
= Conidiocarpus (1)
= Polychaeton (1)
= Scolecoxyphium (1)

Strigopodia Bat.
= Antennatula (2)
= Capnophialophora (1)

Trichopeltheca Bat., Costa & Cif.
= Plokamidomyces (2)
= Trichothallus (2)

Triposporiopsis Yamamoto
= Tripospermum (1)

Chaetothyriaceae

Chaetothyrium Speg.
= Merismella (1)

Zukalia Sacc.
= Kazulia

Dothideaceae

Delphinella (Sacc.) Kze.
= Dothiorella (1)

Didymellina Höhn.
= Heterosporium (2)

Discosphaerina Höhn.
= [?] Cercosporella (1)

Dothidea Fr.
= Asteromellopsis (1)
= Aureobasidium (1)
= Phoma (1)
= Systremmopsis (1)

Gillotia Sacc. & Trott.
= Asteromella vel aff. (1)

Guignardia Viala & Ravaz.
= Asteromella (5)
= Aureobasidium (2)
= Colletotrichella (1)
= Dothiorella (1)
= Hormonema (1)
= Kabatia (3)
= Macrophoma (1)
= Phoma (1)
= Phyllosticta (11)
= Phyllostictina (9)
= Sarcophoma (1)
= Selenophoma (8)
= Selenophomopsis (1)
= Septogloeum (1)

Lasiobotrys Kze.
= Ulocladium vel aff. (1)

Microcyclus Sacc.
= Aposphaeria (1)
= [?] Ascochyta (1)
= Cercospora (1)
= Fusicladium (1)
= Passalora (1)
= Pazschkeella vel aff. (1)

Mycosphaerella Johanson
= Aschochyta (7)
= Asteroma (1)
= Asteromella (4)
= Cercoseptoria (1)
= Cercospora (16)
= Cercosporella (4)
= Cercosporidium (1)
= Cladosporium (4)
= Cylindrosporella (1)
= Fusicladiella (1)
= Lecanosticta (1)
= [?] Marssonina (1)
= Ovularia (1)
= Passalora (1)
= Phaeoisariopsis (1)

= Phloeospora (2)
= Phoma (6)
= Phyllosticta (13)
= Placosphaeria (1)
= Polythrincium (1)
= Ramularia (10)
= Septocylindrium (2)
= Septogloeum (1)
= Septoria (25)
= Stenella (1)
= Stigmina (1)
= Toxosporium (1)

Omphalospora Theiss. & Syd.
= Hendersonia (1)
= Seimatosporium (1)

Plowrightia Sacc.
= Aureobasidium (1)
= Hormonema (1)
= Rabenhorstia (1)

Pringsheimia Schul.
= Aureobasidium vel aff. (1)
= Dothichiza (1)

Scirrhia Nits.
= Acremonium (1)
= Asteromellopsis (1)
= Dothiostroma (1)
= Hadrotrichum (1)
= Lecanosticta (1)
= Phoma (1)

Sphaerulina Sacc.
= Asteromella vel aff. (microconidial) (2)
= Cercospora (1)
= Cytospora (1)
= Septoria (2)

Dothioraceae

Bagnisiella Speg.
= Haplosporella (1)

Dothiora Fr.
= Aureobasidium (1)
= Cytospora (1)
= Dothichiza (5)
= Hormonema (1)

Sydowia Bres.
= [?] Dothichiza (1)
= Hormonema (2)
= Sclerophoma (2)

Dothideales [?]

Englerulaceae

Questieria Arn. (= Schiffnerula Höhn. fide Arx & Müller 1975)
= Questieriella (1)

Rhytidenglerula Höhn.
= Capnodiastrum (1)

Schiffnerula Höhn.
= Mitteriella (1)
= Sarcinella (2)

Parodiopsidaceae

Alina Rac.
= Septoidium (1)
= Sporidesmium (1)

Balladyna Racib.
= Clasterosporium (2)
= Tretospora (1)

Chevalieropsis Arn.
= Septoidium vel aff. (1)

Parodiellina Arn.
= Arnaudia (1)

Neopardia Petr. & Cif.
= Chuppia vel aff. (1)
= Sarcinella vel aff. (1)

Perisporiopsis P. Henn.
= Septoidium (1)

Pilgeriella P. Henn.
= Septoidium (1)

Pseudosphaeriaceae
Leptosphaerulina McAlp.
= Stemphylium vel aff. (1)
= "blastospores (yeast-like)" (1)

Rhytidiella Zal.
= Phaeoseptoria (1)
= unnamed phialidic coelomycete (1)

Trichothyriaceae
Trichothyrium Speg.
= Hansfordiella (1)
= Isthmospora (1)

[?] Dothideales
[?]
Melioliphila Speg.
= Chionomyces (1)
= Eriomycopsis (1)

[?]
Paranectriella (P. Henn.) Piroz.
= Titaea (1)

[?] Dothideales
[?]
Puttemansia P. Henn.
= Guelichia (1)
= Spermatoloncha (1)
= [?] Tetracrium (1)
= Titaea (1)

Hemisphaeriales
Asterinaceae
Asterina Lév.
= Asteromella (2)
= Clasterosporium (1)

Asterodothis Theiss.
= Asterostromina (1)
= Clasterosporium vel aff. (1)

Aulographina Arx & Müller
= Bahusakala (1)
= Thyrinula (1)

Batistinula Arx
= Triposporium vel aff. (1)

Clypeolella Höhn.
= Clasterosporium (1)
= Mitteriella (4)
= Sarcinella (5)

Dimerosporium Fuckel
= Cicinnobella (1)

Eupelte Syd.
= Clasterosporium vel aff. (1)
= Septoidium vel aff. (1)
= Sporidesmium (1)

Maurodothina Arn. ex Piroz. & Shoem.
= Pirozynskia (1)

Prillieuxina Arn.
= Leprieurina (1)

Uleothyrium Petr.
= Septothyrella (1)

Yamamotoa Bat.
= [?] Clasterosporium (1)
or Mitteriella
or Sarcinella

Leptopeltidaceae
Leptopeltopsis Pet.
= Leptothyrium (1)

Pycnothyrium Died.
= Leptothyrium (1)

Thyriopsis Theiss. & Syd.
= unnamed coelomycete (pycnidial) (1)

Microthyriaceae
Dothidella Speg.
= Aposphaeria (1)
= Passalora (1)
= Phyllosticta (2)
= Piggotia (1)
= Placosphaeria (1)

Munkiellaceae
Trabutia Sacc. & Roum.
= Coniella (1)

Vizella Sacc.
= Manginula (2)

Parmulariaceae
Blasdalea Sacc.
= Chrysogloeum (1)

Hysterostomella Speg.
= Poropeltis (1)

Kiehlia Viégas
= Placonema (2)

Melanoplaca Syd. (= Dothidasteroma Höhnel fide Müller & Arx)
= Placomelan (1)

Schizothyriaceae
Schizothyrium Desm.
= Leptothyrium (1)
= Zygophiala (1)

[?]
Cyclopeltis Petr.
= Cyclopeltella (1)

Hysteriales
Hysteriaceae
Arthonia Ach.
= Septocyta (1)

Farlowiella Sacc.
= Acrogenospora (2)

Glyphium Nits. ex Lehmann
= Peyronelia (2)

Hysterium Tode ex Fr.
= Coniosporium (3)
= Sirodesmium (1)
= Sporodesmium (1)

Hysterographium Corda
= Hysteropycnis (1)

Lophium Sacc.
= Papulaspora (1)

Mytilidion Duby
= Septonema (2)

Patellariaceae
Eutryblidiella (Rehm) Höhn.
= Diplodia vel aff. (1)
= Phoma vel aff. (1)

Tryblidiella Sacc. (= Eutryblidiella (Rehm) Höhnel fide Arx & Müller 1975)
= Diplodia (3)

Myriangiales
- Myriangiaceae
  - Agostaea (Sacc.) Theiss. & Syd. (= Anhellia Racib. fide Arx)
    - = Tubercularia (1)
  - Ascomycetella Peck
    - = Articularia (1)
  - Elsinoë Rac.
    - = Sphaceloma (17)
    - = unnamed coelomycete (pycnidial) (1)
- Saccardiaceae
  - Allosoma Syd.
    - = Periconiella (1)
- Saccardinulaceae
  - Xenodium Syd.
    - = Xenodiella (1)
- Seuratiaceae
  - Seuratia Patouillard
    - = Atichia (2)
    - = Myriophysella (1)

Pleosporales
- Botryosphaeriaceae
  - Botryosphaeria Ces. & de Not.
    - = Botryodiplodia (1)
    - = Botryosphaerostroma (1)
    - = Diplodia (1)
    - = Dothiorella (3)
    - = Lasiodiplodia (1)
    - = Macrophoma (3)
    - = Sphaeropsis (5)
- Dimeriaceae
  - Dimerina Theiss.
    - = Ectosticta (1)
  - Dimerium Sacc. & Syd.
    - = Cicinnobella (1)
    - = Ectosticta (1)
- Lophiostomataceae
  - Lophiostoma Ces. & de Not.
    - = unnamed coelomycete (pycnidial) (1)
- Pleosporaceae
  - Acanthostigmella Höhn.
    - = Xenosporium (1)
  - Asteromassaria Höhn.
    - = Coryneum (1)
    - = Scolecosporium (1)
  - Buergenerula Syd.
    - = Rhynchosporina (1)
  - Caryospora de Not.
    - = Asteromella (1)
  - Clathrospora Rabenh.
    - = Alternaria (2)
  - Cochliobolus Drechsler
    - = Bipolaris (4)
    - = Curvularia (4)
    - = Drechslera (6)
  - Comoclathris Clem.
    - = Alternaria (1)
  - Cucurbidothis Petr.
    - = Coniothyrium (1)
  - Cucurbitaria S.F. Gray
    - = Camarosporium (15)
    - = Coniothyrium (1)
    - = Dichomera (1)
    - = Diplodia (8)
    - = Hendersonia (3)

= Leptophoma (1)
= Macrophoma (1)
= Phoma (2)
= Pseudodichomera (1)
= Pyrenochaeta (3)

Curreya Sacc.

= Coniothyrium (1)

Dermatodothis Racib. apud Theiss. & Syd.

= Hendersonia vel aff.

Dictyotrichiella Munk

= Rhinocladiella (1)

Didymosphaeria Fuckel

= Dendrophoma (3)
= Fusicladiella vel aff. (1)
= Periconia (1)

Eudarluca Speg.

= Darluca (2)
= Metabotryon (1)

Gemmamyces Casagrande

= Megaloseptoria (1)

Gibberidea Fuckel

= Pleurostromella (1)

Gilletiella Sacc. & Syd.

= Ascochyta vel aff. (1)

Herpotrichia Fuckel

= Corynespora (1)
= Pyrenochaeta (1)

Karstenula Speg.

= Microdiplodia (2)

Keissleriella Höhn.

= Ascochyta (1)
= Dendrophoma (1)

Leptoguignardia Müller

= Diplodina (1)
= Dothichiza vel aff. (1)

Leptosphaeria Ces. & de Not.

= Alternaria (1)
= Ascochyta (1)
= Ascochytula (1)
= Asteromella (1)
= Camarosporium (4)
= Cladosporium (1)
= Coniothyrium (4)
= Diplodina (1)
= Hendersonia (9)
= Leptophoma (1)
= Microdiplodia (1)
= Pestalotia (2)
= Pestalotiopsis (1)
= Phaeoseptoria (5)
= Phoma (19)
= Phyllosticta (1)
= Rhabdospora (2)
= Septoria (4)
= Stagonospora (4)

Lidophia Walker & Sutton

= Dilophospora (1)

Magnaporthe Krause & Webster

= Nakataea (1)

Massaria de Not.
= Asterosporium (1)
= [?] Cytospora (1)
= Diplodia (1)
= Hendersonia (1)
= Myxocyclus (1)
= Rhabdospora (1)
= Scolecosporium (1)
= Stilbospora (2)

Massarina Sacc.
= Anguillospora (1)
= Dactylella (1)
= Stagonospora (1)

Melanomma Nits. ex Fuckel
= Aposphaeria (3)
= Phoma (1)
= Pseudospiropes (1)

Metasphaeria Sacc. (= [?] Leptosphaeria Ces. & de Not.)
= Diploceras (1)
= Phoma (2)
= Septoria (1)

Muellerites Holm.
= Aureobasidium vel aff. (1)

Ophiobolus Riess
= Acremonium vel aff. (1)
= Asteromella vel aff. (1)
= [?] Coniothyrium (1)
= Phoma vel aff. (1)
= Rhabdospora (1)
= Septoria (1)
= Urohendersoniella (1)
= unnamed hyphomycete with proliferating phialides (1)
= microconidia from ascospores (1)

Otthia Nits.
= Diplodia (2)
= Hendersonia (1)
= Phoma (1)
= Stigmina (1)

Paraphaeosphaeria O. Erikss.
= Coniothyrium (3)

Phaeosphaeria Miyake
= Hendersonia (3)
= Phaeoseptoria (2)
= [?] Phyllosticta (2)
= Septoria (1)

Pleospora Rabenh.
= Alternaria (5)
= Camarosporium (1)
= Coniothyrium (2)
= Dendryphion (1)
= Helminthosporium (1)
= Hendersonia (3)
= Leptophoma (1)
= Microdiplodia (1)
= Phoma (10)
= Stagonospora (1)
= Stemphylium (7)

Podonectria Petch
= Peziotrichum (1)
= Tetracrium (4)
= Tetranacrium (1)
= Volutella (1)

Pseudocochliobolus Tsuda, Ueya. & Nishi.
= Helminthosporium (1)

Pyrenophora Fr.
= Alternaria (3)
= Asteromella vel aff. (1)
= Drechslera (13)
= Helminthosporium (2)
= Phoma (1)

Rhopographus Nits.
= Clasterosporium (1)

Setosphaeria Leonard & Suggs
= Exoserohilum (5)

Thaxteriella Petr.
= Helicoma (1)

Trematosphaeria Fuckel
= Phoma (1)

Trichometasphaeria Munk
= Ascochyta (1)

Tubeufia Penzig & Sacc.
= Helicosporium (3)

Sporormiaceae

Preussia Fuckel
= Phoma (3)

Venturiaceae

Apiosporina Höhn.
= Cladosporium (1)
= Fusicladium (1)
= unnamed coelomycete (pycnidial) (1)

Atopospora Petr.
= Didymochora (1)

Dibotryon Theiss. & Syd.
= Cladosporium vel aff. (1)

Didymella Sacc.
= Aschochyta (5)
= Dendrophoma (1)
= Leptostromella (1)
= Phloeospora (1)
= Phoma (5)
= Phyllostictina (1)
= Plenodomus (1)

Gibbera Fr.
= Helminthosporium (1)
= Phoma (1)
= unnamed hyphomycetes (2)

Phaeocryptopus Naumov
= Rhizophoma sp. (1)
= Rhizosphaera sp. (1)

Platychora Petr.
= Piggotia (1)
= Placosphaeria (1)

Teratosphaeria Syd.
= [?] Dendrophoma (1)

Venturia de Not.
= [?] Cladosporium (1)
= Fusicladium (9)
= Pollaccia (4)
= Spilocaea (1)

Xenomeris Syd.
= Hormonema (1)

REPORT OF THE BITUNICATE COMMITTEE

Prepared by Dr. E. Müller for the Committee:
Drs. von Arx, Müller, Luttrell, Pirozynski and Mr. DiCosmo

The alphabetic list of teleomorph-anamorph connections in bitunicate Ascomycetes, allows one to envisage a classification based on the holomorph. The following arrangement deals mainly with generic names, and the specific connections are not mentioned. The system proposed by von Arx & Müller (1975), with one order and 34 families, is chosen as a basis because it offers an almost complete enumeration of the genera known within these families. Since no detailed systematic arrangement is generally accepted at present, this scheme is considered to be no more than one step toward a more natural classification.

The following arrangement does not include supposed connections unproved by cultural experiments. In some cases genera are mentioned which in cultural experiments did not form anamorphs.

Dothideaceae

Anamorphs pycnidial, in pure culture mostly hyphomycetous (*Hormonema*); conidiogenous cells small, often tapering; conidia basipetal, blastic, hyaline, with a rounded base, 1- to 2-celled.

Spermatial states pycnidial, phialidic; spermatia hyaline, rod-shaped, small.

Dothidea Fr. *Plowrightia* Sacc. *Stylodothis* Arx & Müller	hyphomycetous: *Hormonema* Lagerb. & Melin acervular: *Systremmopsis* Petr. (Loeffler 1957) spermatial: *Asteromellopsis* Hess & Müller
Delphinella (Sacc.) Kuntze *Sydowia* Bres. *Pringsheimia* Schulzer *Dothiora* Fr.	pycnidial: *Dothichiza* Lib. (Froidevaux 1972) hyphomycetous: *Hormonema* Lagerb. & Melin (Hermanides-Nijhof 1977)
Leptoguignardia E. Müller	pycnidial: unnamed, *Dothichiza*-like, conidia 2-celled, (Müller 1955)

Botryosphaeriaceae

Anamorphs pycnidial, in pure culture sometimes dematiaceous (*Hormonema*); conidia basipetal or single, hyaline or pigmented, 1- or 2-celled.

Spermatial morphs pycnidial; spermatia basipetal, hyaline, rod- or dumbbell-shaped.

Botryosphaeria Ces. & de Not.	pycnidial: *Botryodiplodia* Sacc. (incl. *Lasiodiplodia* Griff. & Maubl. *Sphaeropsis* Lév. *Dothiorella* Sacc. spermatial: *Leptodothiorella* Höhn.
Guignardia Viala & Ravaz (van der Aa 1973 Müller 1957, Reusser 1964)	hyphomycetous: *Hormonema* Lagerb. & Melin pycnidial: *Phyllosticta* Pers. & Desm. *Sarcophoma* Höhn. *Selenophoma* Maire *Kabatia* Bub. *Colletotrichella* Höhn. spermatial: *Leptodothiorella* Höhn.

Bagnisiella Speg.	pycnidial: *Haplosporella* Speg.
Trabutia Sacc. & Roum.	*Baeumleria* Petr. & Syd.
Parastigmatea Doidge	*Haplolepis* Syd.
Vestergrenia Rehm	*Phyllosticta* Pers. & Desm.

Myriangiaceae

Anamorphs acervular or sporodochial; conidiogenous cells phialidic, polyphialidic or blastic sympodial; conidia 1-celled, hyaline or pigmented.

Anhellia Rac.	hyphomycetous: *Sphaceloma*-like (described as *Tuberculariа nigra* Stev.)
Elsinoë Rac.	acervular: *Sphaceloma* de Bary
	Melanobasidium Maubl.
Xenodium Syd.	*Xenodiella* Syd. (*Sphaceloma*-like)

Saccardiaceae

Anamorphs acervular or hyphomycetous; conidia blastic, often sympodial, 1- to several-celled, hyaline to brown.

Allosoma Syd.	hyphomycetous: *Periconiella* Sacc.

Schizothyriaceae

Anamorphs acervular or hyphomycetous; conidia blastic, often sympodial, 1- to several-celled, hyaline to brown.

Schizothyrium Desm.	hyphomycetous: *Zygophiala* Mason (Baker et al. 1977)

Leptopeltidaceae

Anamorphs pycnidial; conidia blastic, basipetal, small, hyaline, 1-celled.

Leptopeltopsis Petr.	pycnidial: *Leptothyrium* Kunze ex Wallr.
Dothithyriella Höhn.	
Aulographina Arx & Müller	pycnidial: *Thyrinula* Petr. & Syd.
	hyphomycetous: *Bahusakala* Subr. (only in pure culture)

Holm (1977) restricted the family to the genera *Leptopeltis* (incl. *Dothithyriella*, *Leptopeltopsis*, etc.), *Dothiopeltis* and *Ronnigeria*. The asci were claimed to be unitunicate; but this could not be confirmed by re-examination. The *Leptothyrium* anamorphs of *Leptopeltopsis* and *Dothithyriella* are similar to those of *Guignardia* (e.g., *Selenophoma*). The genus *Leptopeltopsis* must be restricted to species with rather large ascomata, with a covering wall composed of indistinct, small, dark cells. In *Dothithyriella*, *Leptopeltopsis* and some other genera the covering wall is composed of radiate rows of larger, very distinct cells. Only species of these genera are very close to each other.

Ronnigeria on the other hand is intermediate between the Leptopeltidaceae and the Botryosphaeriaceae; it is close to *Parastigmatea* and *Guignardia* (sect. *Discosphaerina*).

Parmulariaceae

Dothidasteroma Höhn. — unnamed, blastic, 1-celled, pigmented conidia

The anamorph mentioned for *Kiehlia* Viégas probably does not belong to that fungus and may well be a hyperparasite.

Asterinaceae

According to the kind of anamorphs three groups of genera can be distinguished:

Group I

Anamorphs pycnidial; conidia blastic, 1-celled, brown (often with a ring-like, hyaline, equatorial zone).

Asterina Lév.
Asterolibertia Arnaud
Lembosia Lév.
— pycnidial: *Asterolibertia* Speg.

Uleothyrium Petr.
— " *Septothyrella* Höhn.
— " *Leprieurina* Arnaud

Prillieuxina Arnaud
— " *Asterostomula* Theiss.

Group II

Anamorphs hyphomycetous; conidia blastic, solitary or percurrent, pigmented, transversely septate or septa cruciately arranged, with truncate base.

Batistinula Arx
Yamamotoa Bat.
Clypeolella Höhn.
— hyphomycetous: *Triposporium* Corda
— " *Mitteriella* Sydow
— " *Sarcinella* Sacc.

Group III

Anamorphs hyphomycetous, conidia blastic, solitary transversely septate, leaving pores after their release.

Asterodothis Theiss.
Eupelte Syd.
— hyphomycetous: *Clasterosporium* Schweinitz
— " *Pirozynskia* Subramanian
— " *Mitteriella*-like (unnamed)

Englerulaceae

Schiffnerula Höhn. — hyphomycetous: *Mitteriella*, *Sarcinella*
Rhytidenglerula Höhn. — pycnidial: *Capnodiastrum* Speg.

Parodiellinaceae

Anamorphs hyphomycetous; conidia blastic, solitary or percurrent; pigmented, transversely or cruciately septate; smaller conidia on denticles also often present.

Parodiellina Arnaud *Pilgeriella* P. Henn. *Alina* Rac. *Perisporiopsis* P. Henn. *Ophioparodia* Petr. & Cif. *Chevaleriopsis* Arnaud *Neoparodia* Petr. & Cif.	hyphomycetous: *Septoidium* Arnaud " *Diploidium* Arnaud (*Sporidesmium*-like)
Balladyna Rac.	" *Tretospora* Ellis (*Clasterosporium*)
Dysrhynchis Clements	" *Septoidium*-like (coremia)

Vizellaceae

Anamorphs pycnidial; conidia blastic, 1-celled, hyaline to brown, sometimes with hyaline band. Spermatial state also present (Swart 1971).

Vizella Sacc.	pycnidial: *Manginula* Arnaud (Hughes 1953) " *Manginula*-like with hyaline conidia (Swart 1971)

Atichiaceae (Seuratiaceae)

Atichia Flotow (=*Seuratia* Pat.)	hyphomycetous: *Actinomma* Sacc. *Myriophysella* Speg.

The many-celled propagula can be considered to be stauroconidia (Meeker 1975).

Arthoniaceae

Arthonia Ach.	pycnidial: *Septocyta* Petr.

Anamorph known only in one example, pycnidial; filiform blastoconidia on elongated conidiogenous cells (Jung 1957).

Patellariaceae

Eutryblidiella (Rehm) Höhn.	pycnidial: *Diplodia* Fr. (macroconidia) " *Phoma* Sacc. (microconidia)

Hysteriaceae

Anamorphs pycnidial or hyphomycetous; conidium ontogeny thallic or blastic; conidia diverse.

Hysterium Tode ex Fr.	pycnidial: *Hysteropycnis* Hilitzer hyphomycetous: *Coniosporium* Link ex Fr.
Hysterographium Corda	pycnidial: *Hysteropycnis* Hilitzer
Farlowiella Sacc.	hyphomycetous: *Acrogenospora* Ell. & Ev.

Lophiaceae

Mytilidion Duby	hyphomycetous: *Septonema* Corda

Lophiostomaceae

Within the genus *Lophiostoma* Ces. & de Not. an unnamed pycnidial anamorph is mentioned by Chesters & Bell (1970).

Pleosporaceae

The Pleosporaceae is a large but rather heterogeneous family. None of the proposed divisions into smaller families has proved to be satisfactory. An arrangement based on the holomorph is difficult because fewer than half of the genera include anamorphs in the life cycles of at least some of the accepted species. The following subdivision into 4 groups is also based on the anamorphs, and is therefore incomplete, but may give some leads toward a more adequate classification.

Group I

Anamorphs hyphomycetous macroconidial, and pycnidial microconidial; macroconidia usually blastic leaving pores after dehiscence, pigmented, rarely remaining hyaline, transversely or muriformly septate; microconidia phialidic, hyaline, small.

Pleospora Rbh.	macroconidial: *Alternaria* Nees ex Fr.
(species with fusiform ascospores	" *Stemphylium* Wallr.
and pycnidial macroconidial	" *Dendryphion* Wallr.
states must be excluded,	
Eriksson 1967b)	microconidial: *Phoma* Sacc.
Comoclathris Clem.	macroconidial: *Alternaria* Nees ex Fr.
Cochliobolus Drechsler	" *Curvularia* Boedijn
	" *Bipolaris* Shoem.
Pseudocochliobolus Tsuda & Ueyama	macroconidial: *Helminthosporium* (Tsuda & Ueyama 1977)
Setosphaeria Leonard & Suggs	" *Exserohilum* Leonard & Suggs
Buergenerula Syd.	" unnamed, *Curvularia*-like
Melanomma Nitschke ex Fuckel	" *Pseudospiropes* Ellis
	microconidial: *Aposphaeria* Berk.
Didymosphaeria Fuckel	macroconidial: *Fusicladiella* Höhn.
(the genus may be heterogeneous)	" *Periconia* Tode ex Fr.
	microconidial: *Dendrophoma* Sacc.
Magnaporthe Krause & Webster	macroconidial: *Nakataea* Hara

Genera probably closely related but having only microconidial (spermatial) conidiomata:

Fenestella Tul.	microconidial: *Phoma* Sacc.
Protocucurbitaria Naumov	" *Phoma* Sacc.

Group II

Anamorphs pycnidial; macroconidia blastic, solitary or basipetal, 1-celled or transversely or muriformly septate, hyaline or pigmented; microconidia (spermatia) usually phialidic; 1-celled, hyaline, small.

Leptosphaeria Ces. & de Not.	macroconidial:	*Camarosporium* Schulz.
	"	*"Hendersonia* Sacc."
	"	*Rhabdospora* Sacc.
	"	*Stagonospora* Sacc.
	microconidial:	*Phoma* Sacc.
Dermatodothis Rac.	macroconidial:	*Hendersonia*-like
Phaeosphaeria Miyake	"	*Hendersonia* Sacc. (incl. *Phaeoseptoria*,
	"	*Septoria* auct. non Fr.)
Gemmamyces Casagrande	"	*Megaloseptoria* Naumov
Eudarluca Speg.	"	*Darluca* Cast. (*Sphaerellopsis* Cooke)
	"	*Metabotryon* Syd.
Otthia Nitschke	"	*Diplodia* Fr.
	"	*Stigmina*-like*
Cucurbitaria S.F. Gray	"	*Camarosporium* Schulz.
	"	*Diplodia* Fr.
	microconidial:	*Phoma* Sacc.
	"	*Pyrenochaeta* de Not.
Keissleriella Höhn.	macroconidial:	*Ascochyta* Lib.
	microconidial:	*Dendrophoma* Sacc.
Gilletiella Sacc. & Syd.	macroconidial:	*Ascochyta*-like
Paraphaeosphaeria O. Erikss.	"	*Coniothyrium* Corda emend. Sacc.**
Curreya Sacc.	"	*Coniothyrium* Corda
Massarina Sacc.***	"	*Stagonospora* Sacc.
	"	*Diplodia* Fr.
	"	*Microsphaeropsis* Höhn.
	microconidial:	*Ceratophoma* Höhn.

Genera probably closely related but having only spermatial anamorphs:

Herpotrichia Fuckel	microconidial:	*Pyrenochaeta* de Not.
Trematosphaeria Fuckel	"	*Phoma* Sacc.
Gibberidea Fuckel	"	*Pleurostromella* Petr.

Group III

Anamorphs hyphomycetous, conidia usually many-celled, occasionally helicoid, hyaline or slightly pigmented, solitary or sympodial.

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* The anamorph of *Otthia lisae* (de Not.) Sacc. forms large stromatic complexes in pure culture. On these, four-celled, pigmented conidia are formed.

** *Coniothyrium* is closely related to *Camarosporium*; it is considered to be macroconidial.

*** *Massarina* seems to be heterogeneous; the type species belongs here but some of the other species are different in morphology. According to their anamorphs these are placed in group III.

Thaxteriella Petr.	hyphomycetous:	*Helicoma* Corda
Tubeufia Penz. & Sacc.	"	*Helicosporium* Nees
Podonectria Petch	"	*Tetracrium* Henn.
Melioliphila Speg.	"	*Eriomycopsis* Speg.
Paranectriella Höhn. (*Poltiella* Petr. 1974)	"	*Titaea* Sacc.
Puttemansia P. Henn.	"	*Titaea* Sacc.
	"	*Guelichia* Speg.
Massarina Sacc.	"	*Anguillospora* Ingold
Acrospermum Tode ex Fr. (Eriksson 1967a, Pirozynski 1976)	"	*Dactylaria* Sacc.
	"	*Virgariella*-like (Webster 1956)

Group IV

Anamorphs acervular or pycnidial; conidia blastic, percurrent or solitary, large, transversely or muriformly septate, pigmented, mostly distinctly thick-walled, with truncate base.

Splanchnonema Corda	*Stegonosporium* Corda
Pleomassaria Speg.	*Prosthemium* Kunze ex Fr.
Asteromassaria Höhn.	*Scolecosporium* Lib.
Pseudovalsa Ces. & de Not.	*Coryneum* Nees ex Fr.
Prosthecium Fres.	*Stilbospora* Pers. ex Mérat

Genera included in the Pleosporaceae sensu Arx & Müller (1975) having no conidial anamorphs (only examples which have been examined in pure culture):

Clathrospora Rbh.	*Macrovalsaria* Petr.
Entodesmium Riess	*Massaria* de Not.
Leptospora Rbh.	*Dothivalsaria* Petr.
Nodulosphaeria Rbh.	*Valsaria* Ces. & de Not.
Ophiobolus Riess	

Pseudosphaeriaceae

Anamorphs hyphomycetous; conidia blastic leaving pores (poroconidia), pigmented, transversly or muriformly septate.

Leptosphaerulina McAlpine	hyphomycetous:	*Stemphylium* Wallr.
Pyrenophora Fr.	"	*Drechslera* Ito

Mycoporaceae

Arthopyrenia Mass.	unnamed, pycnidial, phialidic (Riedl 1977)

Mycosphaerellaceae

Hyphomycetous and pycnidial anamorphs are known which -- as in the Pleosporaceae -- can be used to separate the holomorphs into groups:

Group I

Anamorphs pycnidial; conidia blastic, solitary or basipetal, ellipsoid, fusiform or filiform, hyaline, 1-celled or with transverse septa.

Spermatial state pycnidial, phialidic, spermatia rod-shaped: *Asterostomella* Pass & Thüm.

Mycosphaerella Johanson *Sphaerulina* Sacc.	pycnidial: *Septoria* Fr. (incl. *Phleospora*)
Didymella Sacc.	" *Ascochyta* Lib. " *Phoma* Sacc.
Microcyclus Sacc.	" *Pazschkeella* Syd. (*Ascochyta*-like)
Gillotia Sacc.	" *Aposphaeria*-like

Group II

Anamorphs hyphomycetous; conidia blastic, solitary or in acropetal chains, cylindrical, ellipsoidal, fusiform or filiform, 1-celled or with transverse septa, hyaline or pigmented.

Spermatial state the same as in group I: *Asteromella* Pass. & Thüm.

Mycosphaerella Johanson	hyphomycetous: *Cercospora* Fres. " *Cercosporella* Sacc. " *Cercoseptoria* Petr. " *Ramularia* Unger " *Ovularia* Sacc. " *Cladosporium* Link ex Fr.* " *Heterosporium* Cooke " *Polythrincium* Kunze ex Fr.
Sphaerulina Sacc.	" *Cercospora* Fres.
Microcyclus Sacc.	" *Passalora*-like / *Cercospora*-like

Stigmateaceae

Anamorphs hyphomycetous or pycnidial (not typical members); conidia blastic, cicatrized, single, sympodial, basipetal or in acropetal chains, usually with brown or more typically with greenish or olive pigments, amerosporous or with transverse septa.

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* *Cladosporium* is considered in a more restricted sense (cf. Ellis 1971, 1976); *Heterosporium*, *Karakulinia* and *Hormoconis* Arx & de Vries are segregated.

Venturia de Not. sensu Sacc.	hyphomycetous:	*Spilocaea* Fr.
	"	*Pollaccia* Bald. & Cif.
	"	*Fusicladium* Bon.
	"	*Karakulinia* Golov. (segregate of *Cladosporium*)
Gibbera Fr.	"	*Strumellopsis* Höhn.
Antennularia Rchb. (=*Protoventuria* Berl.)	"	*Karakulinia* Golov.
Xenomeris Syd.	"	*Karakulinia* Golov.
Apiosporina Höhn.	"	*Fusicladium* Bon.
Lasiobotrys Kunze ex Fr.	"	*Cladosporium*-like (*Karakulinia* ?)
Parodiella Speg.*	microconidial/spermatial:	*Scleroparodia* Petr.
Teratosphaeria Syd.*		unnamed, pycnidial with rod-shaped spermatia.

Dimeriaceae

Dimerium Sacc.	microconidial, pycnidial:	*Cicinnobella* P. Henn.
	" "	*Ectosticta* Speg.
Dimerina Theiss.	" "	*Ectosticta* Speg.

Both genera may be related to *Eudarluca* (Pleosporaceae) or *Didymella* (Mycosphaerellaceae).

Capnodiaceae sensu lato

Von Arx & Müller (1975) treated all "pyrenomycetous" sooty molds in a single family, Capnodiaceae. Hughes (1976) on the other hand, distinguished several -- mostly new -- families, which are mainly based on characters of the hyphae, the teleomorph and the diverse anamorphs.

Euantennariaceae

genera: *Euantennaria* Speg., *Trichopeltheca* Bat. et al.
anamorphs: hyphomycetous, phialidic: *Hormisciomyces* Bat. & Nasc.
Plokamidomyces Bat. et al.
blastic: *Antennatula* Strauss
Trichothallus Stev.
Capnokyma Hughes

Metacapnodiaceae

genera: *Metacapnodium* Speg., *Ophiocapnodium* Bat. & Cif.
anamorphs: hyphomycetous, phialidic: *Capnophialophora* Hughes
sympodial: *Capnobotrys* Hughes
Capnocybe Hughes
poroconidial: *Capnosporium* Hughes
Hormiokrypsis Bat. & Nasc.

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* not typical Stigmateaceae

Antennulariellaceae

genera: *Antennulariella* Woron., *Achaetobotrys* Bat. & Cif.
anamorphs: hyphomycetous, blastic: *Capnodendron* Hughes
pycnidial, microconidial: *Antennariella* Bat. & Cif.

Capnodiaceae sensu stricto

genera: *Capnodium* Mont., *Scorias* Frl., *Phragmocapnias* Theiss. & Syd.
anamorphs: pycnidial: *Fumagospora* Arnaud
(conidium ontogeny not clear): *Phaeoxyphiella* Bat. & Cif.
Polychaeton (Pers.) Lév.
Conidiocarpus Woron.
Scolecoxyphium Cif. & Bat.

Aithaloderma H. & P. Syd
anamorphs: hyphomycetous, synnematal: *Ciferrioxyphium* Bat. & Maia
anamorphs: pycnidial: *Cylindroxyphium* Bat. & Cif.

Genera not included in one of the above families.

Brooksia Hansf. — pycnidial: *Capnogoniella* Bat. & Cif.
hyphomycetous: *Hiospira* R.T. Moore

Dennisiella Bat. & Cif. — hyphomycetous: *Microxiphium* (Harvey ex Berk. & Desm.) Thüm.

Limacinula (Sacc.) Höhn.

The Triposporiopsidaceae are considered to belong to the Sphaeriales (Hughes 1976), whereas the Oplotheciaceae Bat. & Cif. represent a part of the Sphaeriaceae (Müller & von Arx 1973).

Chaetothyriaceae

Chaetothyrium Speg. — pycnidial: *Merismella* Syd.

According to Hughes (1976) this seems to be the only connection within the Chaetothyriaceae; *Chaetothyrium concinnum* Syd. (1926) may not be a typical species of *Chaetothyrium*.

Trichothyriaceae

Trichothyrium Speg. — hyphomycetous: *Isthmospora* Stev. (Hughes 1953)

Herpotrichiellaceae

Dictyotrichiella Munk — hyphomycetous: *Exophiala* Carmichael (de Hoog 1977)

Sporormiaceae

Preussia Fuckel — pycnidial: *Phoma*-like
Westerdykella Stolk

DISCUSSION

Earlier attempts have been made to connect the Ascomycetes with the form system of Fungi Imperfecti (Deuteromycetes). Tubaki (1958) and Müller (1971) failed to find such an association between the then accepted orders, but we do, however, know of many clear connections at the generic level. In the preceding list the genera of bitunicate Ascomycetes with known anamorphs are arranged in the families delimited by von Arx & Müller (1975). No anamorphs are known in the six families: Brefeldiellaceae, Mesnieraceae, Zopfiaceae, Micropeltidaceae, Microthyriaceae and Piedraceae. In addition, the known connections within the following twelve families do not seem sufficient for any comment: Parmulariaceae, Vizellaceae, Atichiaceae, Arthoniaceae, Lophiaceae, Lophiostomaceae, Mycoporaceae, Dimeriaceae, Chaetothyriaceae, Trichothyriaceae, Herpotrichiellaceae and Sporormiaceae.

1. Dothideaceae

In this family two groups of genera can be distinguished: those with small, usually unilocular stromata and those with large, pustulate stromata containing numerous small loculi. In the first group the anamorphs usually develop in separate stromata, in the second group they are formed in young stromata which later develop the teleomorph. The conidia (and spermatia) develop singly or mostly in basipetal succession on small, often deliquescent, conidiogenous cells. In culture dark hyphae develop on which the conidia are also formed basipetally and often form slimy masses (anamorph genus *Hormonema*).

2.. Botryosphaeriaceae

Similar cultural forms and similar dark mycelia indicate a relationship to the Dothideaceae. The conidia are formed in pycnidial conidiomata on short, occasionally percurrent conidiogenous cells in basipetal succession and have a truncate or a rounded base. The conidia are usually larger than those of the Dothideaceae. Often an additional spermatial state, with rod- or dumbbell-shaped spermatia formed on awl-shaped phialides, is present. Some species also include *Hormonema* growth phases.

3. Myriangiaceae

Anamorphs are known only in *Elsinoë* and two related genera; the conidia develop basipetally or sympodially on awl-shaped, phialide-like cells in sporodochia (or acervuli).

4. Leptopeltidaceae

The *Leptothyrium* anamorphs known in species with radiate ascomata (belonging to *Dothithyriella*, etc.) indicate a relationship to the Botryosphaeriaceae with similar anamorphs (e.g., the anamorph genus *Selenophoma*).

6. Asterinaceae/Englerulaceae

The genera classified in these families may be re-classified according to the anamorphs as follows:

Group I

Asterina, Lembosia, Prillieuxina, Rhytidenglerula and similar genera include pycnidial anamorphs, and the hyphae are rather narrow and brown.

Group II

Clypeolella, Schiffnerula and some other genera are characterized by broad, dark, thick-walled hyphae on which usually many-celled, pigmented conidia are formed singly or percurrently.

Group III

Asterodothis and *Eupelte* differ in having conidia leaving pores after their release (poroconidia).

7. Parodiellinaceae

The hyphae and the anamorphs are similar to those of the *Clypeolella* group of the Asterinaceae. The teleomorphs are also rather similar.

The anamorphs also show some similarities to those of some Stigmateaceae (e.g., *Pollaccia, Spilocaea*), to some Massariaceae (e.g., *Coryneum, Stegonosporium*) and to some Amphisphaeriaceae (e.g., *Sporocadus/Stigmina, Pestalotia*).

10. Pleosporaceae/Pseudosphaeriaceae

In this large family several different kinds of anamorphs are known, and these allow the recognition of at least four groups. The classification of the many taxa which lack anamorphs, however, is often difficult or impossible.

Group I (Pleosporaceae s.str.)

This group includes the taxa with usually large, many-celled conidia which develop sympodially and leave pores or thickened scars, or both, after release (anamorph genera *Alternaria, Stemphylium, Drechslera, Curvularia, Bipolaris, Exserohilum*). Some other anamorph genera with conidia which leave denticles with pores after release, such as *Nakataea* and *Pyricularia*, seem to be close to *Exserohilum*.

Group II

This unnamed group includes the taxa with anamorphs forming pycnidial conidiomata. The conidia usually develop basipetally on short conidiogenous cells and have a rounded or truncate base. At least some of the genera classified in this group may be related to Mycosphaerellaceae with similar anamorphs, belonging to anamorph genera such as *Phoma* and *Ascochyta*. Similar anamorphs are also known in the Sporormiaceae and the Dimeriaceae.

Group III (Acrospermataceae Rehm)

This family was re-introduced by Eriksson (1967a) and extended by Pirozynski (1976), and mainly comprises Ascomycetes parasitic on other fungi, with light, fleshy ascomata and hyaline many-celled, often filiform ascospores. The anamorphs are mucedinaceous and the sympodial conidia are usually many-celled and often curved. The family may be related to the Clavicipitaceae and the Hypomycetaceae of the Sphaeriales, which have similar teleomorphs but usually include phialidic anamorphs.

Group IV (Massariaceae Winter)

This family comprises bark-inhabiting fungi with large ascomata with a dark wall composed of

small cells, and with thick-walled, many-celled, usually pigmented ascospores. The anamorphs are pycnidial or acervular and the large, pigmented, often many-celled conidia are formed singly on conidiogenous cells which are often percurrent. Von Arx has proposed the addition of the genera *Pseudovalsa*, *Prosthecium* and *Massariovalsa*, hitherto usually classified in Diaporthaceae.

11. Mycosphaerellaceae

Although some anamorphs belong to either the Hyphomycetes or Coelomycetes, a separation into different groups would not be opportune. Von Arx (1949) demonstrated that the separation of the genus *Mycosphaerella* into different groups, as proposed by Klebahn (1918), and based on the generic names of the anamorphs (*Septoria*, *Cercospora*, *Ramularia*) would not be helpful. A rather large number of species have no known anamorph, while other species produce more than one (e.g., conidia and spermatia). Some isolates of *Mycosphaerella tassiana* include a *Cladosporium* anamorph, but isolates collected in cold areas (arctic, alps) are identical except in that they have no such anamorph. There are intermediates between the coelomycetous genus *Septoria* and the hyphomycetous genus *Cercospora*, classified as *Cercoseptoria* and under other names.

12. Stigmateaceae

This family can be easily recognized by the characters of the teleomorph as well as the anamorph, when this is present. The latter is uniform in spite of different kinds of conidiogenesis (acropetal chains, sympodial, or percurrent) and the conidia (and the ascospores) are similar in size, shape and pigmentation.

The genera *Parodiella* and *Teratosphaeria*, with pycnidial anamorphs, will have to be transferred to the Mycosphaerellaceae or to group IV of the Pleosporaceae.

Commentary on the Bitunicate Committee Report by Dr. Luttrell

I have added Dr. Pirozynski's name to the list of the Committee members, since he participated voluntarily in the discussions -- he was, I believe, the only volunteer in the entire group. Dr. Müller is convener, chairman, chief contributor and recorder; I sat on a stool to see what he was doing. He insisted that I give this report because he thinks I speak English. The problem is that the results are written in Gothic -- and the decisions were reached in Swiss.

We do have some examples of 100% correlation. In the Brefeldiellaceae there is one genus, and it does not produce conidia: 100% negative correlation. The Atichiaceae contains one genus, all species of which produce strange stauroconidia: 100% correlation. This is an indication that if you get the group small enough..... We did, however, come up with a number of genuinely interesting points: I'll deal with them family by family.

Dothideaceae: A family with a high degree of correlation between anamorphs and teleomorphs. But even in a small group like this we can encounter problems. 1) A distinction must be made between spermatial states and conidial states: this may be very difficult, because it is not easy to establish function. Nevertheless we must try, because in many cases two anamorphs have been reported. One of these is usually a spermatial morph and must be considered apart from the conidial morph. 2) Sometimes in the Dothideaceae a third anamorph has been reported -- 'Hormonema', 'Aureobasidium'. We solved this problem by calling it a growth phase which often develops in culture after ascospore germination. Here we have several 'anamorphs' which all contribute to the pattern, and there is a high degree of physical correlation between large, obvious ascostromata, and equally stromatic pycnidial anamorphs.

Botryosphaeriaceae: there is good correspondence between morphology of ascospores and that of conidia formed in pycnidioid conidiomata.

Myriangiaceae: a small and rather atypical family; here we find the only anamorphs in all of the Bitunicates that could be called phialidic but are not formed in pycnidial conidiomata. Phialidic conidia formed in pycnidia are more broadly distributed.

Asterinaceae: Von Arx & Müller (1975) recognized three families. But von Arx now thinks that they were not natural groups. So we went ahead and amalgamated them. Then when we examined this larger group from the point of view of the anamorphs, we decided that there are three groups. But they are not the same three groups we started with! This kind of re-thinking may lead to a reorganization of the group.

Pleosporaceae: a major group which from the point of view of the teleomorphs cannot, so far as we can see, be subdivided; but some encouragement may be derived from the anamorphs. In one group of genera we have conidia produced in basipetal chains in pycnidia (*Phoma, Diplodia* etc.). In another group we have the formation of poroconidia. Another group including *Podonectria, Thaxteriella,* and *Tubeufia* have pseudothecia with light-coloured walls, unusual among Bitunicates: this group has unusual blastic anamorphs which are hyperparasitic: just the kind of result we might have hoped for. All in all, our results in the Pleosporaceae are surprisingly encouraging.

Mycosphaerellaceae: most of the known anamorphs in this family belong to one teleomorph genus, *Mycosphaerella*; and they are amazingly diverse. *Mycosphaerella* is a very large genus, and we might suggest, both from its size and the diversity of its anamorphs, that it is in need of subdivision. Yet from one extreme to the other there appears to be a continuum of variation. Valleys there may be between the peaks, but they aren't deep enough -- any hourglass figure you drew would have to be more tightly corseted to be convincing. So the anamorphs suggest heterogeneity, but don't show us where the lines should be drawn.

Stigmateaceae: as in the preceding family, most of the known anamorphs belong to a single teleomorph genus, *Venturia*, and again these anamorphs are rather diverse. This is a puzzling feature of both families. Dr. Madelin discussed this problem at the end of Chapter 6.

Capnodiaceae: This group has been extensively worked by Hughes (1972, 1976), who concluded that there are four families. The Capnodiaceae sensu stricto characteristically produce pycnidial anamorphs. We don't know exactly how the conidia are formed, but this may not

matter because the peculiar structure of the pycnidia again reflects the peculiar structure of the ascomata; so this is probably a good correlation. Hughes actually used the anamorphs as a basis for his taxonomic decisions in subdividing a large complex of fungi which was itself ecologically circumscribed. This is an excellent example of the kind of thing we hope to see happening all across the fungal spectrum, and I will use it to close this commentary on an optimistic note.

We fully intend to correct, expand and update the lists of teleomorph-anamorph connections given above. I urge the mycological community to send corrections, reports of new connections, and suggestions for improving our presentation in the next edition, to me: Dr. Bryce Kendrick, Department of Biology, University of Waterloo, Waterloo, Ontario Canada N2L 3G1.

And now, I invite you to sample the contents of Volume 2, which leans fairly heavily on the Basidiomycetes (including the Uredinales) and their anamorphs, but also has a few surprise packages concerning the 'yeasts' and the Zygomycetes, coverage of anamorph-teleomorph ecology, the methodology of making connections, a discussion of fossil fungi, and finally a return to the nomenclatural problems raised by pleomorphic fungi.....

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